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Land-use change, protected area effectiveness, and wildlife dynamics in post-Soviet European Russia

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Abstract

Within the Anthropocene era, our world faces a biodiversity crisis that is mainly caused by human-induced environmental changes such as land-use change and the overexploitation of wildlife. Protected areas are a cornerstone of the global conservation efforts and particularly important for preserving large mammals. Increasing human impact and continued loss and fragmentation of wildlife habitats inside and outside protected areas strongly affect their effectiveness and conservation value, especially during times of socio-economic and institutional shocks with reduced financial and human resources for nature conservation. The breakdown of the Soviet Union in 1991 was such a shock and the overall aim of this thesis was to contribute to a better understanding of how this shock affected land use, protected area effectiveness, and wildlife dynamics in European Russia. European Russia served as a representative area for such a study as it is a human-dominated region, which harbors large mammal species and a long-established network of scientific protected areas providing long-term biodiversity data. The overall aim of this thesis was assessed by using a broad range of data and interdisciplinary approaches to monitor and evaluate changes in land use and hunting pressure, protected areas, wildlife habitats, and species population dynamics in post-Soviet times. The results of this thesis revealed that the socio-economic and institutional shock following the breakdown of the Soviet Union resulted in reduced land-use pressure due to widespread farmland abandonment and overall lowered rates of forest logging in European Russia. Protected areas played an important role in halting threats to biodiversity and benefitted from increased large mammals' habitat within their zone of interaction. Wildlife dynamics were significantly affected by land-use change and hunting pressure in post-Soviet times. The findings of this thesis provide a valuable contribution to support biodiversity monitoring and overcome knowledge gaps on biodiversity conservation.

Zusammenfassung

Im Zeitalter des Anthropozäns ist unsere Welt mit einer Biodiversitätskrise konfrontiert, welche vor allem durch vom Menschen bedingte Umweltveränderungen verursacht wird, wie beispielsweise Landnutzungswandel und die Ausbeutung von Flora und Fauna. Naturschutzgebiete sind ein Eckpfeiler der globalen Bemühungen des Umweltschutzes und besonders wichtig für den Erhalt von Großsäugern. Fortschreitender menschlicher Einfluss sowie zunehmender Verlust und die Zerteilung von Lebensräumen innerhalb und außerhalb von Naturschutzgebieten beeinflussen deren Effektivität und Wert für den Umweltschutz stark, besonders in Zeiten sozioökonomischer und institutioneller Schocks mit reduzierten finanziellen und personellen Ressourcen für den Umweltschutz. Der Zusammenbruch der Sowjetunion im Jahr 1991 war solch ein Schock und das übergeordnete Ziel dieser Doktorarbeit war es, besser zu verstehen, wie dieser Schock die Landnutzung, die Effektivität von Naturschutzgebieten und die Populationsdynamik von Wildtieren beeinflusst hat. Der europäische Teil Russlands bot sich deshalb als repräsentatives Untersuchungsgebiet an, da es eine vom Menschen stark beeinflusste Region ist, welche Lebensraum für Großsäuger aufweist sowie ein Netzwerk von alten, wissenschaftlichen Naturschutzgebieten besitzt, die über Langzeitdaten zur Biodiversität verfügen. Das übergeordnete Ziel dieser Doktorarbeit wurde mittels umfassender Datensätze und der Anwendung interdisziplinärer Ansätze bearbeitet, um die Veränderungen in Landnutzung, Jagddruck, Naturschutzgebieten, Lebensräumen und Populationsdynamiken von Wildtieren in post-sowjetischer Zeit zu beobachten und auszuwerten. Die Ergebnisse dieser Doktorarbeit ergaben, dass der sozioökonomische und institutionelle Schock nach dem Zusammenbruch der Sowjetunion einen verringerten Landnutzungsdruck zur Folge hatte, bedingt durch die weit verbreitete Aufgabe von Landwirtschaft und generell abnehmende Raten von Waldeinschlag im europäischen Teil Russlands. Naturschutzgebiete spielten eine wichtige Rolle beim Schutz der Biodiversität und profitierten von vergrößerten Lebensräumen für Großsäuger innerhalb ihres Interaktionsraumes. Wildtierpopulationsdynamiken waren in post-sowjetischer Zeit wesentlich beeinflusst von Landnutzungswandel und Jagddruck. Diese Forschungsergebnisse leisten einen wertvollen Beitrag zur Unterstützung des Biodiversitätsmonitorings sowie zum Schließen von Wissenslücken im Biodiversitätsschutz.

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Introduction

1 Human impact on global biodiversity

1.1 Land-use change and hunting as drivers of the global biodiversity crisis

Humans have been permanently shaping the Earth and the 'Anthropocene era' (Crutzen and Stoermer 2000) is dominated by accelerated human population growth, increasing per-capita consumption, and changes in human diet triggering widespread land-use change and the degradation and loss of biotic and abiotic resources (Machovina et al. 2015; Steffen et al. 2015). Global biological diversity, which is defined as "the variability among living organisms from all sources including, among others, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (UN 1992, Article 2), is experiencing a rapid decline with vertebrate population sizes reduced by more than 50% from 1970 to 2010 (Butchart et al. 2010; WWF 2014) and an even more dramatic loss when accounting for invertebrate species extinction, too (Régnier et al. 2015). In the coupled human-environment system, biodiversity is mainly threatened due to human-induced environmental changes such as land-use change, overexploitation, invasive species spread, and climate change (Sala et al. 2000; Rands et al. 2010). Because biodiversity underpins many ecosystem services and has an intrinsic value, the conservation of biodiversity is an important and well-accepted goal (Myers et al. 2000; Brooks et al. 2006; Rands et al. 2010; Cardinale 2012). In 2010, the United Nations announced the 'Decade on Biodiversity' for the period 2011-2020, and related to that the parties of the Convention on Biological Diversity (CBD) adopted the 'Aichi Biodiversity Targets', which aim to reduce future biodiversity loss (UNEP CBD COP 2010). In this regard, to further research how humans are impacting biodiversity is important in order to support global conservation efforts.

Land-use change is one of the main drivers of the current biodiversity crisis and the devastating changes in terrestrial ecosystems (Sala et al. 2000; Foley et al. 2005), leading to the loss and degradation of wildlife habitats worldwide. Land-use change affects biodiversity directly, for example, via habitat loss or habitat fragmentation or via ecosystem recovery, but also indirectly, via enhanced access for poachers, invasive species spread or reduced water availability (Foley et al. 2005; Brook et al. 2008). The dominating global trend is increasing land-use pressure via the expansion of agricultural land and land-use intensification due to the growing global demand on food and biofuel (McLaughlin 2011). Important frontiers of land-use change can be found in the tropical forests, where agricultural areas are expanded for soybean, palm oil or cattle, for example, in the Amazon (Macedo et al. 2012), the African rain forest (Mayaux et al. 2013), and in Southeast Asia (Carrasco et al. 2014). Yet also other ecoregions are affected, for example, in Latin America, due to the conversion of pastures to cropland (Graesser et al. 2015). These frontiers often overlap with areas of high biodiversity concern (Kehoe et al. 2015). At the same time, another common land-use change is decreasing land-use pressure due to extensive farming and the abandonment of agricultural land, such as in Europe, USA, and in Latin America (Cramer et al. 2008; Meyfroidt and Lambin 2011; Plieninger et al. 2016). However, wildlife species respond to changes in land-use intensity due to both the intensification and the abandonment of agriculture (Cremene et al. 2005). Abandoned agricultural fields or pastures often transition to unmanaged grassland or shrubland with regrowing trees due to natural succession. Farmland abandonment can lead to the rewilding of the landscape (Navarro and Pereira 2012) and this 'passive restoration' (Benayas et al. 2009) may especially favor species that are wide-ranging and rely on well-connected habitats, such as large mammals (Smit et al. 2015), and may provide opportunities for conservation. Yet it also may threaten species relying on open habitats in agroecosystems (Plieninger et al. 2014). Nevertheless, it is unclear how land-use change in combination with other threats on wildlife is affecting habitats and species populations, and a better understanding is urgently needed to identify effective conservation strategies and ultimately transition to a more sustainable future.

The human-driven overexploitation of wildlife is a second major driver of the current biodiversity crisis. Human kind has always been exploiting wildlife via hunting for edible and inedible parts, trophy or medical ingredients. Today, many wildlife species are threatened with extinction due to intensified legal or illegal (i.e., poaching) hunting (Ripple et al. 2015), which are tremendously affecting wildlife population dynamics and may lead to 'empty' ecosystems such as forests or seas (Redford 1992; Worm et al. 2009; Stokstad 2014). Particularly the overexploitation of large mammals can be very crucial for ecosystems because trophic cascades, i.e., "reciprocal predator-prey effects that alter the abundance, biomass or productivity of a population community or trophic level across more than one link in a food web" (Pace et al. 1999), can be triggered. This may increase wildfire risk or promote nonnative species invasion (Estes et al. 2011), and may even become more critical for forest ecosystems in certain regions than the immediate effects of climate change (Abernethy et al. 2013). Often, land-use change contributes to increasing hunting pressure, for example, via providing access to hunting grounds (Laporte et al.

2007). However, the interaction between the overexploitation of wildlife and human-induced changes in wildlife habitat remains weakly understood, and more research is needed to inform conservation actions for each factor separately as well as the combined effects to halt biodiversity loss.

1.2 Role of protected areas

Protected areas are a cornerstone of the global conservation efforts, aiming at maintaining wildlife and ecosystems at various scales (Margules and Pressey 2000; Pressey et al. 2014). The International Union of Conservation of Nature (IUCN) described a protected area as "clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values" (IUCN 2016a). IUCN defined seven categories of protected areas based on the respective management objectives, ranging from 'strict nature reserves' (IUCN category Ia) with strict biodiversity protection to 'protected areas with sustainable use of natural resources' (IUCN category VI) with permitted sustainable land use (IUCN 2016b). The global network of protected areas is currently comprising more than 209,000 terrestrial and marine protected areas, and covering about 15% of the terrestrial land and inland water areas (20.6 million km^2; Juffe-Bignoli et al. 2014), which accounts for less than half of the area globally used for agriculture (FAOSTAT 2013). Due to the prevailing biodiversity crisis and the strong human impact on the world's ecosystems in the Anthropocene era, there is an increasing need for conservation (Rands et al. 2010; Caro et al. 2012). Within the Aichi Biodiversity Targets, protected areas are an important immediate and long-term mean to maintain biodiversity and crucial ecosystems. Nevertheless, the international efforts to safeguard biodiversity by means of protected areas are criticized for the insufficiency of the postulated activities (Pressey et al. 2014; Tittensor et al. 2014; Ripple et al. 2015) and for not halting the ongoing biodiversity loss in terrestrial and marine habitats (Mora and Sale 2011). Thus, the question remains how protected areas are facing global threats in order to fulfil their postulated aims.

Protected areas have to overcome a variety of threats lowering their effectiveness in biodiversity conservation. The effectiveness of protected areas can cover different aspects, for example, the capability of reducing threats to the protected ecosystem (Andam et al. 2008), management activities in reaching conservation goals (Ervin 2003; Hockings 2003) or the representation of species diversity within their boundaries (Rodrigues et al. 2004). However, there are protected areas insufficiently preventing the degradation of ecosystems and poorly maintaining biodiversity within their territory, often in times of insecure socio-economic or institutional conditions. These 'paper parks' (McNeely et al. 1994) are defined as unmanaged protected areas suffering from deficient funding and human resources (Stolton and Dudley 1999; Blackman et al. 2015). Furthermore, protected areas worldwide are threatened by increasing human impact within their boundaries, for example, illegal forest logging and poaching (Fa and Brown 2009; Knorn et al. 2012) or climate change, which may push species' ranges out of protected areas (Hannah et al. 2007). The question remains how effective protected areas are in halting threats to biodiversity, particularly in times of reduced funding and resources, for example, in the aftermath of rapid shocks in socio-economic or institutional conditions.

Even if protected areas were effective, they are embedded within larger ecosystems and closely connected to their surroundings in a 'zone of interaction' via complex ecological, socio-economic, and cultural interrelations (Hansen and DeFries 2007; DeFries et al. 2010). The zone of interaction embraces the protected area itself and its surrounding area up to various sizes depending on either definition or spatial discrimination. It can cover, for example, a catchment area, an administrative unit or a particular buffer around the protected area. What happens outside protected areas often concurrently affects the biodiversity inside their territory. Increasing human population, changes in the intensity and spatial range of land use, and hunting in the protected areas' surroundings impact habitats and species richness and may further threaten endangered species within protected areas, particularly in human-dominated landscapes (Plumptre et al. 1997; Novaro et al. 2000; Wittemyer et al. 2008; Joppa et al. 2009; Butsic et al. 2012; Martinuzzi et al. 2015). Increasing human impact and continued loss and fragmentation of wildlife habitats outside protected areas can lead to the isolation of protected areas, what strongly impairs their effectiveness and conservation value (DeFries et al. 2005; Struhsaker et al. 2005; Newmark 2008). While covering the same administrative size, isolated protected areas have a smaller effective area compared to protected areas that are connected to wild areas in their surroundings. In isolation, essential interrelations with the surrounding area cannot be maintained, which can make protected area borders population sinks (Woodroffe and Ginsberg 1998) and particularly affects wide-ranging large mammals (Newmark 2008). Land-use change and human impact outside of protected areas are affecting biodiversity within protected areas and are reducing their conservation value; however, the linkages between protected areas and their surroundings remain weakly understood, especially during times of rapid socio-economic and institutional change.

1.3 Large mammals

Large mammals, i.e., terrestrial mammals with a body mass exceeding a certain, not clearly defined threshold, for example, 20 kg (Vynne et al. 2011) or 100 kg (Ripple et al. 2015), are strongly affected by human pressure. First, land-use change strongly affects large mammals because they are usually wide-ranging and require large and well-connected areas of intact habitat (Ripple et al. 2014). Second, these species are often hunted or poached for their meat, trophy, medical parts or because they conflict with people or land use (Milner-Gulland et al. 2003a; Ripple et al. 2015). Large mammals are particularly threatened by overhunting as they are relatively slowly reproducing (Ripple et al. 2015). Especially at the edges of protected areas, different land uses frequently compete and conflicts between humans and wildlife often decrease animal abundance (Woodroffe and Ginsberg 1998; Newmark 2008; Martinuzzi et al. 2015). However, large mammals rely on protected areas as a refuge, and are often dependent on protected areas' surroundings, particularly in human-dominated landscapes with intensive land use and high hunting pressure and often only small administrative areas of protection (Galanti et al. 2006; Carter et al. 2012).

Among large mammals, herbivores, i.e., plant-eating animals, and carnivores, i.e., members of the order carnivora, play crucial roles in ecosystems and are particularly threatened by extinction due to land-use change and overexploitation (Dirzo et al. 2014). Large herbivores and carnivores are crucial to ecosystems since they ensure ecological connections and interactions due to their large home ranges (Dirzo et al. 2014; Ripple et al. 2015). They also provide important ecosystem services as they are essential for nutrient cycling, regulating fire regimes, disease control, limiting invasive species spread, and maintaining biodiversity (Estes et al. 2011; Ripple et al. 2015). Furthermore, large herbivores are considered 'ecosystem engineers' because they are maintaining and expanding habitat heterogeneity via grazing, browsing, or trampling, they are ensuring food security for humans, and represent the main food source for large carnivores, usually apex predators at the top of the food web (Ripple et al. 2015). When they vanish, trophic cascades can be triggered, impacting entire ecosystems (Estes et al. 2011; Abernethy et al. 2013; Palmer et al. 2015).

Large mammals are often umbrella species, i.e., "species whose conservation is expected to confer protection to a large number of naturally co-occurring species" (Roberge and Angelstam 2004), and ensuring their survival may benefit many other species. Large herbivores and carnivores are also often regarded as charismatic and used as flagship species for conservation campaigns, and may thus represent shortcuts for conservation managers (Kuemmerle et al. 2010; Yackulic et al. 2011). Long-term data on the occurrence and abundance of large mammal species, however, are usually scarce (Magurran et al. 2010). Evaluating such data is particularly interesting in light of better understanding how socio-economic and institutional shocks affect wildlife habitats and population dynamics within and outside of protected areas.

1.4 Protected areas and wildlife during times of shocks

Rapid shocks in socio-economic or institutional conditions, such as revolutions, economic crises, large-scale diseases or wars can result in fundamental transformations of human-environment systems (Hostert et al. 2011; Pongratz et al. 2011). First, these rapid shifts can trigger land-use change with increasing forest logging in some regions such as in the case of the breakdown of the Soviet Union, when forest disturbances increased after 1991 in former socialist countries (Kuemmerle et al. 2007). At the same time, relaxing land-use pressure is also possible, for example, during wartimes (Hanson et al. 2009; Baumann et al. 2014) or after large-scale diseases (Yeloff and van Geel 2007). Overall, land-use change following drastic socio-economic or institutional changes may lead to threats and opportunities for biodiversity conservation (Fischer et al. 2012). Second, socio-economic shocks may affect nature conservation. On the one hand, such events can lead to the rapid expansion of a country's protected area network, for example, after the colonial era in Africa or following the expansion of the European Union (Schreurs 2004; Gaston et al. 2008; Radeloff et al. 2013). On the other hand, they may result in lower levels of control, increased poverty, and illegal resource use, and thus degrade the effectiveness of protected areas (McNeely et al. 1994). Losing their income possibilities after a shock event, local livelihoods often increase their hunting activities to get food or sell meat for profit, while organized poaching and trophy hunting may be facilitated due to increasing risks for patrols in protected areas during wartimes (Plumptre et al. 1997; Dudley et al. 2002; UNODC 2012). How rapid shifts in socio-economic and institutional conditions affect wildlife populations through the interacting drivers of land-use change and overexploitation, however, remains weakly understood.

2 The breakdown of the Soviet Union and its effects on nature conservation in European Russia

In 1991, the collapse of the Soviet Union, the formerly largest country in the world, led to a shift from a socialist state-controlled to a market-based economy and to rapid changes in socio-economic and institutional conditions (Mroz and Popkin 1995). In the Russian Federation, hereafter Russia, the repeated severe economic crises following the breakdown of the Soviet Union and the Russian fiscal crisis in 1998 shaped the socio-economic situation in post-Soviet Russia. It was characterized by increasing poverty due to low individual incomes and increasing unemployment in the 1990s (Mroz and Popkin 1995), continued rural depopulation (Ioffe and Nefedova 2004), impairment of human health and welfare (Herzfeld et al. 2014), and a high level of corruption (Marxsen 2005). Moreover, during Soviet times, efforts in nature conservation and environmental protection were mainly subordinated to socialist industrial development. This often resulted in the overexploitation of natural resources due to the high economic dependence on oil, gas and metal exports and still prevailing environmental pollution legacies throughout Russia (Henry and Douhovnikoff 2008; Hanson 2009). Understanding the effects of the socio-economic and institutional shock on changes in land use, hunting pressure, and protected areas after the breakdown of the Soviet Union is crucial for understanding how nature conservation in European Russia was affected in post-Soviet times.

The drastic changes in socio-economic and institutional conditions resulted in widespread changes in land use, mainly affecting agroecosystems and forests. The most widespread land-use change following the upheaval in 1991 was the abandonment of agricultural land. This happened in many areas of post-socialist Eastern Europe (Estel et al. 2015) such as the Carpathian ecoregion (Kuemmerle et al. 2008), Ukraine (Baumann et al. 2011), the Baltic countries (Peterson and Aunap 1998; Prishchepov et al. 2012a) or in the steppe grasslands of Kazakhstan (Kraemer et al. 2015). In Russia, particularly European Russia was affected because it exhibits the main part of agricultural land (Ioffe et al. 2004). During Soviet times, agricultural production was mainly organized in big state or collective farms (Ioffe et al. 2004). After the collapse in 1991, former markets within the Soviet Union were suddenly lost, capital investments were reduced followed by de-mechanization, and state subsidiaries for petrol and fertilizer were cancelled (Trueblood and Arnade 2001; Prishchepov et al. 2013). This resulted in reduced input for agricultural production and amplified inefficiency of collective farms. Increasing subsistence farming at the household level in post-Soviet times could not balance the reduced production capacities of large farms (Wegren and Nikulin 2016) and agricultural output decreased strongly. Besides wheat and other corn production (Schierhorn et al. 2014), livestock farming also drastically declined (e.g., 65% decline of cattle in the time period 1990-2010; ROSSTAT 2011), turning Russia into a leading meat importer, particularly from South America (Prikhodko and Davleyev 2014). At the same time, abandoned land was also reclaimed again, for example, more than 50% of the abandoned croplands in Kazakhstan have been recultivated since the year 2000 (Kamp et al. 2015b). This recultivation may close existing yield gaps (Schierhorn et al. 2014), but also threatens wildlife populations depending on recovering habitats on abandoned fields such as steppe birds (Kamp et al. 2015b). Changes in forest cover occurred with varying dynamics in the former socialist states after the collapse of the Soviet Union. Increasing intensity of forest harvest occurred in parts of European Russia (Potapov et al. 2012), West Siberia (Dyukarev et al. 2011), Poland, Slovakia, and Ukraine (Kuemmerle et al. 2007). At the same time, logging intensity decreased elsewhere, for example, in other areas of European Russia (Baumann et al. 2012; Sieber et al. 2013), amended by forest expansion on abandoned farmland, especially in Eastern Europe (Potapov et al. 2015). In this regard, European Russia offers the unique potential to better understand the effects of the collapse of the Soviet Union on land-use change and to learn about the subsequent effects on wildlife habitats and populations.

The Russian network of protected areas is one of the oldest and largest networks worldwide (Danilina 2001; Krever et al. 2009). Today, about 11% of the Russian terrestrial territory is covered by protected areas of different protection level (IUCN and UNEP-WCMC 2015). Similar to the protected area network in the United States, Russian protected areas are smaller in size in regions of higher human density such as in European Russia compared to the Asian part (Parks and Harcourt 2002). The first modern Russian protected area was established at Lake Baikal in 1916 (Barguzinsky zapovednik; Tschernikin 1999), and since then the Russian network of protected areas has experienced great changes (Spetich et al. 2009). It is organized at three management levels, i.e., federal, regional, and local, and covers seven different types of protected areas (Krever et al. 2009). The so-called ‘zapovedniks’ are strictly protected, scientific nature reserves, regulated at the federal level (IUCN category Ia) and aiming at scientific monitoring and nature protection (Spetich et al. 2009). Zapovedniks offer valuable long-term biodiversity data, providing exceptional information on the relationship between human impact and wildlife.

Since 1940, standardized biodiversity accounts of each zapovednik, the Chronicles of Nature (Летописи природы, Letopisi prirody), have been annually published (Ostergren and Hollenhorst 2000). They in part rely on winter track counts (Зимний маршрутный учёт, Zimny marshrutny ushet) that represent unique, long-term time series of wildlife population data, which are based on decades of field work and are unparalleled in the world (Spetich et al. 2009). The collapse of the Soviet Union brought a ‘hot moment for conservation‘ (Radeloff et al. 2013) since about 114 new protected areas and national parks were planned to be established in Russia in the early 1990s, but only 23 were finally founded (Safonov 2013). Nevertheless, this was a glimmer of hope for that time because after 1991, an eroding infrastructure due to severe cuts in funding and an institutional restructuring posed significant challenges for nature conservation in Russia (Wells and Williams 1998; Fiorino and Ostergren 2012). The repeated reorganization of the Russian protected area management at the federal level (e.g., in 2000, the Russian State Ministry for Environmental Protection ‘Goskomekologiia’ was merged into the Russian Ministry for Natural Resources) awakened fears of overexploitation of natural resources within protected areas, and resulted in an excess of bureaucratization at the local level (Crotty and Rodgers 2012). Besides these institutional changes and post-Soviet land-use change, illegal resource use became widespread in post-Soviet times, further threatening protected areas and their surroundings. Particularly illegal logging in the Russian Northwest (Ottitsch et al. 2005; Bank 2006), the Russian Far East and in Southern Siberia (Vandergert and Newell 2003; Kabanets et al. 2013) as well as poaching (Ostergren and Shvarts 2000; Ottitsch et al. 2005) are prevailing today, and are thus challenging conservation efforts to maintain biodiversity. How these trends combine to affect the effectiveness of Russia’s protected areas after the breakdown of the Soviet Union remains poorly understood, especially in the surroundings of protected areas.

Russia harbors a high biodiversity across many ecoregions including expansive wild areas inhabited by large mammal species (Dinerstein 1994; Amirkhanov 1997; Olson and Dinerstein 1998). After the breakdown of the Soviet Union, hunting of abundant wildlife was increasingly uncontrolled and poaching became widespread (Ostergren and Shvarts 2000; Sidorovich et al. 2003; Safonov 2013), posing additional threats to biodiversity and nature conservation. Most large mammal species experienced decreasing population sizes in Russia during this time (Bragina et al. 2015a), mainly due to poaching, and some species such as saiga antelope (*Saiga tatarica*; Milner-Gulland et al. 2003b) were brought to the edge of extinction. So far, research on threatened wildlife species in the regions of the former Soviet Union mainly covered charismatic large mammals, for example, Amur (Siberian) tiger (*Panthera tigris altaica*; Tian et al. 2011), Amur (Far Eastern) leopard (*Panthera pardus orientalis*; Hebblewhite et al. 2011), Persian leopard (*Panthera pardus saxicolor*; Breitenmoser et al. 2007) or bison (*Bison bonasus*; Bleyhl et al. 2015). There are few places in the world where drastic and widespread changes in socio-economic and institutional conditions and land use have occurred while long-term biodiversity data are available. Russia is such a place and scientific evaluations of Russian biodiversity data have almost not been carried out in the Western literature, especially regarding large mammal species with extensive distribution ranges. The immense potential of this data is to enable analyzing long-term changes in habitats and wildlife populations, and to better understand the effect of socio-economic and institutional shocks on protected area effectiveness and biodiversity that has not been explored much.

3 Motivation, research questions, and approaches

The ongoing global biodiversity crisis has increased the need of better understanding how ecosystems and wildlife are affected by human impact to promote actions for improved nature conservation and to halt biodiversity loss. Land-use change and hunting are among the main threats to biodiversity, and their relative effects on changes in wildlife dynamics remain unclear, especially during times of socio-economic and institutional shocks, which may provide additional challenges to nature conservation. Further research is needed to explore how human impact is affecting wildlife habitats and species populations to learn about the relative importance of land-use change and hunting, and to assess how effective protected areas are in preserving their inherent ecosystems, particularly in times of reduced human and financial resources. In this regard, European Russia is a well-suited and representative area for such a study. The breakdown of the Soviet Union in 1991 resulted in severe changes in socio-economic and institutional conditions that certainly affected the human-dominated landscape in European Russia including protected areas, which harbor large mammal species in their zone of interaction and a long history of scientific biodiversity monitoring.

The overall aim of this dissertation was to contribute to a better understanding of how the socio-economic and institutional shock of the breakdown of the Soviet Union in 1991 affected land use, protected area effectiveness, and wildlife dynamics in European Russia. This was addressed in three overarching research questions and assessed using a broad range of data and interdisciplinary approaches to monitor and evaluate changes in land use and hunting pressure, protected areas, wildlife habitats, and species population dynamics (Figure I-1).

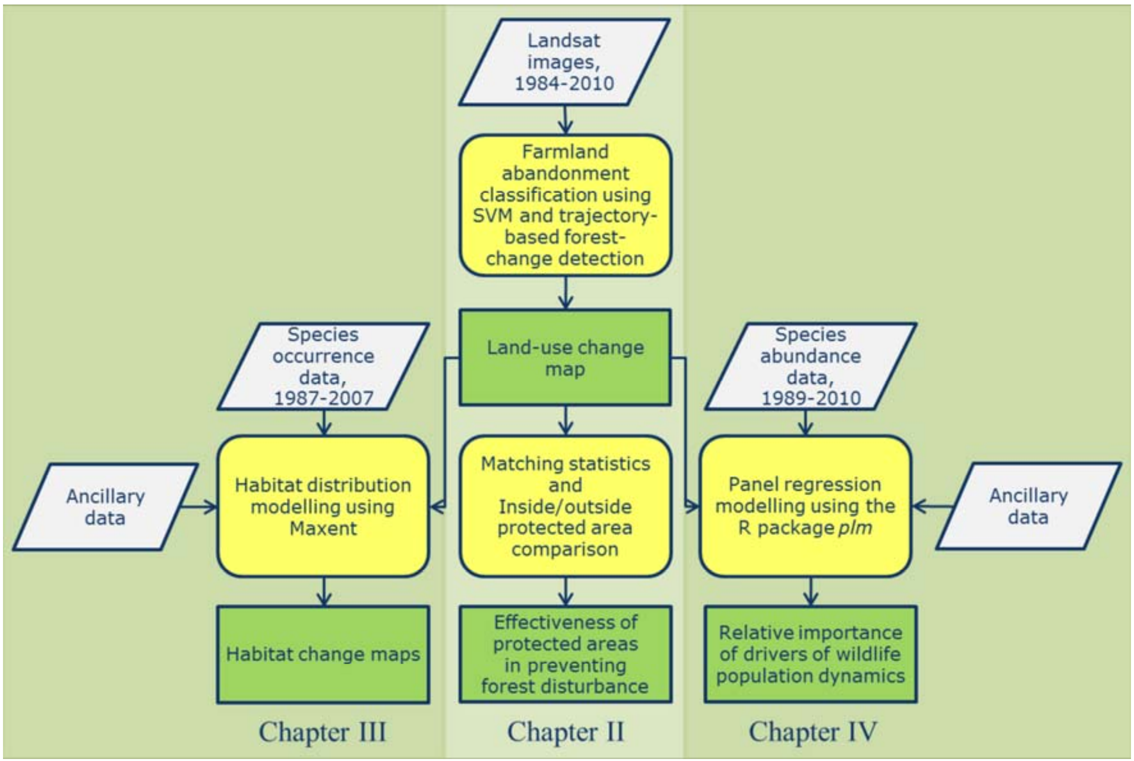

Figure I-1: Workflow highlighting input data, approaches, and results of the three research chapters (Ancillary data = socio-economic statistics, biophysical data, etc.; SVM = Support vector machine).

The breakdown of the Soviet Union resulted in altered socio-economic and institutional settings, which triggered land-use change, i.e., changes in farmland and forest cover, in European Russia. This translates into the first central research question of my dissertation, which was addressed in detail by two objectives:

Research question I: *How did the breakdown of the Soviet Union affect land use in European Russia?*

- *Objective 1: To map spatial patterns and quantify farmland abandonment*
- *Objective 2: To map spatial patterns and quantify annual rates of forest-cover change*

Earth observation and remote sensing techniques provide amplitude of data and methods to assess land-use change at various spatial and temporal scales and Landsat satellite images are widely used to map and monitor land cover, land use, and related changes (Wulder et al. 2008). Based on a long time series of Landsat satellite images (1984-2010, TM4, TM5, and ETM+), multi-temporal change detection was applied to map spatial and temporal patterns of post-Soviet land-use change in temperate European Russia. A support vector machine (SVM) classifier (Huang et al. 2002) was used to identify and quantify changes in farmland, i.e., arable land and managed grassland, with a focus on farmland abandonment. A trajectory-based forest disturbance detection (Healey et al. 2005) was adopted to identify and quantify changes in forest cover due to forest disturbances and natural succession on abandoned farmland.

Socio-economic and institutional shocks are particularly challenging times for protected areas in terms of effectiveness because weak law enforcement may spur illegal activities, thus undermining conservation targets. Furthermore, land-use change in the surroundings of protected areas affects wildlife species within protected areas, particularly large mammals, which rely on large and well-connected habitats. Evaluating the effectiveness of protected areas in preventing land-use change and assessing changes in large mammals' habitat is therefore important and essentially contributes to nature conservation. This translates into the second central research question of my dissertation, which was addressed in detail by two objectives:

<u>Research question II</u>: *How effective have protected areas been in post-Soviet European Russia?*

- *Objective 1: To assess the effectiveness of protected areas in preventing forest loss*
- *Objective 2: To evaluate the changes in large mammals' habitat within and outside of protected areas*

The effectiveness of protected areas in preventing forest loss within their boundaries was assessed twofold. First, by comparing annual rates of forest disturbance within and outside two strictly protected areas in temperate European Russia, Oksky and Mordovsky State Nature Reserves. Second, by deriving relative probabilities of forest loss within and outside these protected areas while controlling for their potentially non-random allocation in the broader landscape using matching statistics (Andam et al. 2008). Furthermore, large mammal species, e.g., wild boar (*Sus scrofa*), moose (*Alces alces*), and wolf (*Canis lupus*), are occurring within and outside of Oksky State Nature Reserve. Long-term field data for these species were used in time-calibrated species distribution models (Phillips et al. 2006) in order to learn about the habitat selection of large mammals and to assess changes in habitat availability due to post-Soviet land-use change in the protected area's zone of interaction.

Besides widespread land-use change, the rapid shifts in socio-economic and institutional conditions following the breakdown of the Soviet Union also triggered changes in hunting pressure. Moreover, it remains largely unknown how the interaction between land-use change and hunting was affecting the abundance of large mammals in post-Soviet European Russia. This translates into the third central research question of my dissertation, which was addressed in detail by two objectives:

<u>Research question III</u>*: How did the breakdown of the Soviet Union, and here in particular the interaction between land-use change and hunting, affect wildlife dynamics in European Russia?*

- *Objective 1: To determine the changes in and drivers of large mammals' populations*
- *Objective 2: To assess the relative importance of land-use change and hunting on fluctuations in species' population dynamics*

Long-term abundance data of wild boar were available for protected and unprotected areas in Ryazan Oblast, a federal subject of the Russian Federation in temperate European Russia. Applying a panel regression model (Croissant and Millo 2008), these data were first evaluated to explore the population trends of wild boar and to determine the significant drivers of population dynamics. Second, these data were evaluated to assess the relative importance of factors related to human impact on driving population dynamics while controlling for natural mortality.

4 The study area in European Russia

European Russia encompasses the western part of the Russian Federation until the Ural Mountains in the East, which discriminate Europe from Asia. The study area is located in the human-dominated temperate region within the Eastern European Plain. It is characterized by mostly flat terrain at low altitudes and a temperate continental climate (Priklonsky and Tichomirov 1989; Tereshkin et al. 1989). Analyses of long-term climate data of local strictly protected areas showed a decreasing trend in continentality due to increases in temperature, especially in winter, and precipitation (Onufrenya 2003, 2012). The study area is located within the temperate broadleaf and mixed forest biome at the intersection of two ecoregions: the sarmatic mixed forests and the East European forest steppe (Olson et al. 2001;Figure I-2). In the sarmatic mixed forests, boreal forests with pine (*Pinus sylvestris*) and spruce (*Picea abies*) as well as mixed temperate forests including oak (*Quercus robur*) and linden (*Tilia cordata*) are dominating (Priklonsky and

Tichomirov 1989; Tereshkin et al. 1989). Here, the Meshchera lowlands, a flat and marshy area with poor soils on a former glacial lake bed (Lydolph 1990), characterize the western part of the study area. On large river banks, livestock farming on managed grassland is common. The East European forest steppe is a mosaic of forests, which includes oak, linden, Norway maple (*Acer platanoides*), and common hazel (*Corylus avellana*), and meadow steppe vegetation (Chibilyov 2002). This ecoregion is strongly influenced by human land use due to fertile soils with chernozems and kashtanozems and characterized by large areas of arable land and scarce natural woodlands (Chibilyov 2002).

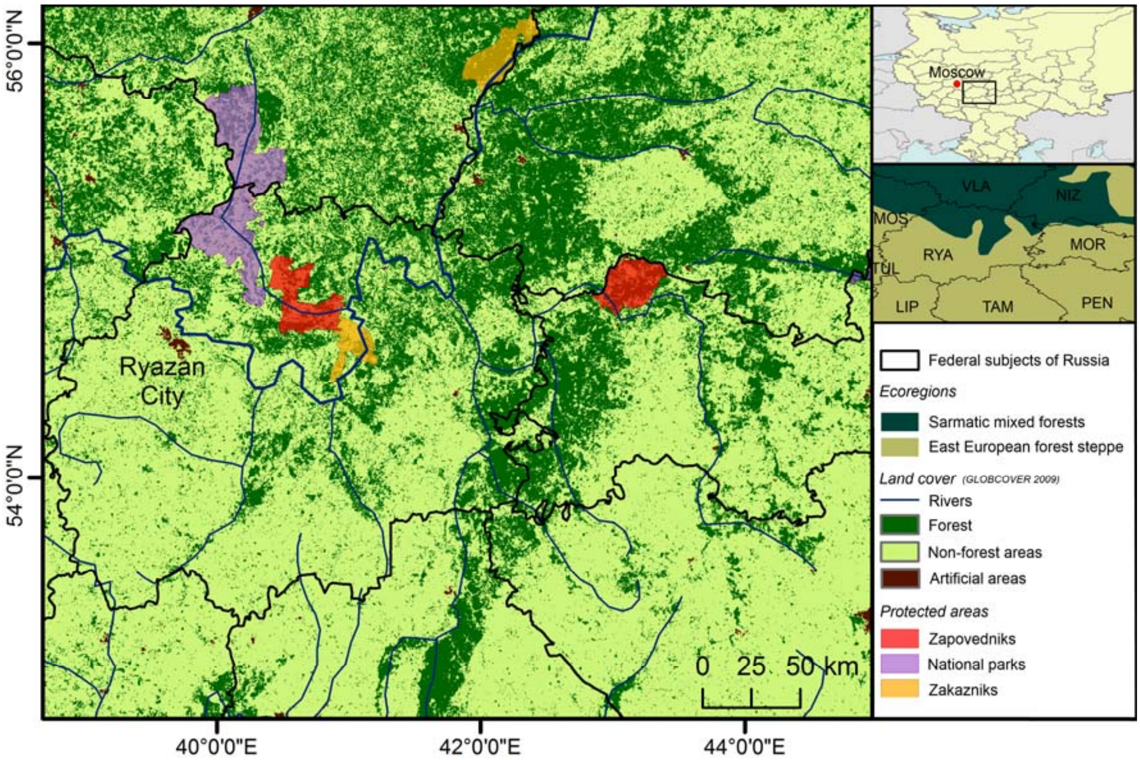

Figure I-2: Study area in European Russia (Federal subjects: RYA = Ryazan Oblast, VLA = Vladimir Oblast, NIZ = Nizhny Novgorod Oblast, MOR = Republic of Mordovia, PEN = Penza Oblast, TAM = Tambov Oblast, LIP = Lipetsk Oblast, TUL = Tula Oblast, MOS = Moscow Oblast).

The study area covers about 75,000 km² within seven federal subjects of the Russian Federation, yet mainly Ryazan Oblast and the Republic of Mordovia (Figure I-2). The breakdown of the Soviet Union in 1991 resulted in strongly changing socio-economic conditions in this agrarian area with, for example, decreasing human population due to the continued rural depopulation, and increasing unemployment rates due to the privatization and decollectivisation of the farm system (Brooks and Gardner 2004; Ioffe and Nefedova 2004).

There are several federally managed protected areas within the study area. The two strictly protected, scientific nature reserves (i.e., zapovedniks; Figure I-2), Oksky and Mordovsky

State Nature Reserves, were established in 1935 and 1936, respectively, and unify a long history of studying and protecting biodiversity (Priklonsky and Tichomirov 1989; Tereshkin et al. 1989). Other types of protected areas are national parks (IUCN II) and zakazniks, i.e., wildlife sanctuaries (IUCN III; IV). The study area is inhabited by large mammal species, for example, brown bear (*Ursus arctos*), which is listed in the Russian Red List, wild boar, which is an important game species in Russia (Baskin and Danell 2003), moose, and wolf.

The study area is representative for large parts of European Russia. Its location at the junction of two ecoregions, which are both highly human-dominated, the long history of nature conservation within protected areas, the abundance of large mammals, and the socio-economic and institutional shock that occurred after the breakdown of the Soviet Union motivate this thesis to learn about the interrelated changes in land use, the effectiveness of protected areas, and the changes in habitat and population dynamics of large mammals.

5 Structure of this thesis

This thesis is designed as a cumulative dissertation, consisting of an introduction chapter (Chapter I), three research chapters (Chapters II-IV), and a synthesis and conclusion chapter (Chapter V). The three research chapters of my dissertation (see list below) address each at least one research question posed above and correspond to a research article either published in (Chapter II and III) or submitted to (Chapter IV) international, peer-reviewed journals.

Chapter II

Sieber, A., Kuemmerle, T., Prishchepov, A.V., Wendland, K.J., Baumann, M., Radeloff, V.C., Baskin, L.M., Hostert, P. (2013). Landsat-based mapping of post-Soviet land-use change to assess the effectiveness of the Oksky and Mordovsky protected areas in European Russia. *Remote Sensing of Environment* 133, 38-51.

Chapter III

Sieber, A., Uvarov, N.V., Baskin, L.M., Radeloff, V.C., Bateman, B.L., Pankov, A.B., Kuemmerle, T. (2015). Post-Soviet land-use change effects on large mammals' habitat in European Russia. *Biological Conservation* 191, 567-576.

Chapter IV

Sieber, A., Baskin, L.M., Prishchepov A.V., Goryantseva, O.V., Onufrenya, M.V., Markina, T.A., Ivanchev, V.P., Radeloff, V.C., Uvarov, N.V., Kuemmerle, T. (submitted). Hunting and land-use change effects on wild boar population dynamics in European Russia during post-Soviet times. *Ecological Applications.*

Chapter II:
Landsat-based mapping of post-Soviet land-use change to assess the effectiveness of the Oksky and Mordovsky protected areas in European Russia

Remote Sensing of Environment, Volume 133, June 2013, Pages 38-51

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Abstract

Land-use and land-cover change (LULCC) is the main cause of the global biodiversity crisis and protected areas are critical to prevent habitat loss. Rapid changes in institutional and socio-economic conditions, such as the collapse of the former Soviet Union in 1991, often trigger widespread LULCC. Yet, it is unclear how effective protected areas are in safeguarding habitat within them during such periods of rapid LULCC. Our goal here was to map changes in forest cover and agricultural lands from 1984 to 2010 in order to assess the effectiveness of two strictly protected areas, Oksky and Mordovsky State Nature Reserves, in temperate European Russia. We analysed dense time series of Landsat images for three Landsat footprints and applied a support vector machines classification and trajectory-based change detection to map forest disturbance. We then used matching statistics to quantify the effectiveness of the protected areas. Our analyses highlighted considerable post-Soviet LULCC in European Russia. The LULCC maps revealed disturbances on 5.02 % of the total forest area, with strongly declining disturbance rates in post-Soviet times. We also found that 39.89 % of the agricultural land used in 1988 was abandoned after 1991, leading to widespread forest regrowth. Oksky and Mordovsky State Nature Reserves had a significantly lower probability of forest disturbance (-0.1 to -3.5 % lower) in comparison to their surrounding areas. This suggests that protected areas were relatively effective in limiting human-induced forest disturbance in European Russia, despite lower levels of control and an eroding infrastructure for nature protection. Moreover, we found drastic land-cover changes, particularly forest regrowth, in the surroundings of these protected areas, highlighting conservation opportunities. Protected areas can play a key role in biodiversity conservation during periods of rapid LULCC, and remote sensing coupled with matching statistics provide important tools for monitoring the success and failure of conservation efforts.

1 Introduction

Global biodiversity is declining rapidly (Butchart et al. 2010), with land-use and land-cover change (LULCC) and overexploitation being two of the main drivers of these losses (Millennium Ecosystem Assessment 2005; EEA 2007; Gonzalez et al. 2011). LULCC affects biodiversity via habitat loss, degradation, and fragmentation (Lindenmayer and Fischer 2006), and as such represents a challenge for biodiversity conservation in areas where land use is intensifying (Kleijn et al. 2009; Rudel et al. 2009; Fischer et al. 2012). However, land-use change can also result in ecosystem recovery, for example, where shifting socio-economic conditions trigger agricultural abandonment (Kuemmerle et al. 2008; Benayas et al. 2009; Meyfroidt and Lambin 2011). Both processes can co-occur, leading to complex outcomes. This is particularly the case for regions where socio-economic shocks (e.g., revolutions, wars, or epidemics) take place, frequently leading to both illegal resource use (Greenpeace 2008; Kuemmerle et al. 2009), and the abandonment of agriculture (Yeloff and van Geel 2007; Hostert et al. 2011; Pongratz et al. 2011). Better understanding the complex interrelations of socio-economic shocks and LULCC is therefore important to identify efficient biodiversity conservation strategies.

Protected areas are a cornerstone of global conservation efforts (Margules and Pressey 2000; Rodrigues et al. 2004; Dudley et al. 2010). Many protected areas are both directly and indirectly affected by human land use, either because they permit at least some human use within their territory (Radeloff et al. 2010), or because they are surrounded by intensive land use (Curran et al. 2004). A particular protected area is embedded within a larger ecosystem via a ‘zone of interaction’ (DeFries et al. 2010), highlighting that there are both strong ecological and socio-economic interactions between protected areas and their surroundings (Hansen and DeFries 2007). These interrelations raise the question how socio-economic shocks, which may erode the infrastructure for conservation (Henry and Douhovnikoff 2008) and which are known to lead to drastic LULCC, affect protected areas.

One of the most dramatic socio-economic shocks in recent times, in terms of area affected, was the collapse of the Soviet Union in 1991. The subsequent transition from a socialistic-planning to market-oriented economic systems strongly affected forestry and agricultural sectors in almost all succession states of the Soviet Union (Krankina and Dixon 1992), and this triggered drastic land-use changes. In Russia, the largest country of the former Soviet

Union, forest harvesting changed considerably (Torniainen et al. 2006), with decreasing logging rates in some areas, for example, European Russia (Potapov et al. 2011; Wendland et al. 2011; Baumann et al. 2012) and southern central Siberia (Bergen et al. 2008), but also increased illegal logging, for example, in the Russian Far East and eastern Siberia (Vandergert and Newell 2003). Overall though, logging patterns in post-Soviet Russia are not well understood (Houghton et al. 2007). In terms of agriculture, the dominant trend of land-use change was the widespread abandonment of farmland throughout Eastern Europe (Peterson and Aunap 1998; Ioffe et al. 2004; Kuemmerle et al. 2011a; Prishchepov et al. 2013). Reforestation on abandoned farmland may have increased the total forest area in European Russia (Baumann et al. 2012), but where and how much abandonment and reforestation happened remains also unclear.

Russia is also a particularly interesting country to investigate the effects of LULCC on protected areas because Russia harbours exceptional biodiversity (Russian Academy of Sciences & Ministry of Natural Resources of the Russian Federation 2001) and has a well-established and extensive network of protected areas. Today, there are more than 11,000 protected areas covering about 200 million ha, equalling about eleven percent of the Russian territory (Krever et al. 2009; IUCN and UNEP-WCMC 2011). Of these protected areas, 102 are zapovedniks, (i.e., strictly protected, scientific state nature reserves, IUCN category Ia) (IUCN and UNEP-WCMC 2011), established solely for conservation and scientific monitoring. Zapovedniks, particularly the older ones (i.e., the first zapovednik was founded in 1892, Danilina 2001), preserve unique landscapes across different ecoregions in Russia. More zapovedniks are located in European Russia, but these are usually smaller in size due to the higher human population densities and the long history of intensive land use (Spetich et al. 2009). The collapse of the Soviet Union in 1991 resulted in severe funding cutbacks for conservation efforts, and many protected areas are today short in personnel, equipment, and financial capacity (Wells and Williams 1998). At the same time, weak law enforcement resulted in increasing illegal resource use in the post-Soviet period, for example, illegal logging (Morozov 2000; Eikeland et al. 2004) and poaching (Milner-Gulland et al. 2003b), thus posing new challenges for conservation. Given these challenges, it remains unclear whether Russia’s protected areas remained effective in the post-Soviet period. Likewise, we currently lack knowledge on how LULCC affected protected areas and their surroundings in Russia.

Assessing the spatial patterns of post-Soviet LULCC is challenging though because data on changes in forest cover, such as forest inventory data, are often not easy to access, out of date, unreliable, available only in aggregated form, or lack information on illegal logging (Filer and Hanousek 2002; Houghton et al. 2007). Similarly, data on changes in agricultural land use are often not available for larger areas and do not provide information on potential forest succession. Remote sensing has therefore become a key technology for monitoring post-Soviet LULCC (Peterson and Aunap 1998; Bergen et al. 2008; Kovalskyy and Henebry 2009; Kuemmerle et al. 2011a). In the past, most LULCC approaches were limited by the availability and the cost of data, and mostly focused on bi-temporal change detection. With the recent opening of the USGS Landsat archives, dense time series of satellite imagery are now available for many regions in the world, spanning 30 years of land-use change including the entire post-Soviet period. Newly developed approaches of time series analyses allow assessing changes in a pixel's spectral-temporal profile or of proxies derived from the original spectral data (Huang et al. 2010; Kennedy et al. 2010) to better identify both rapid and gradual LULCC. This provides new opportunities to better understand the effects of socio- economic shocks, which happen at distinct points in time on land systems and on the effectiveness of conservation (Griffiths et al. 2012).

Likewise, remote sensing has been instrumental to measure the effectiveness of protected areas (Curran et al. 2004; Kuemmerle et al. 2007; Gorsevski et al. 2012; Knorn et al. 2012). Such assessments have traditionally often relied on comparing LULCC inside and outside protected areas. This is problematic considering that protected areas are regularly established in marginal or remote areas and that the protection may lead to spillover effects, for example, increased land use pressure in the surrounding areas (Andam et al. 2008). Simply comparing rates of LULCC inside and outside of protected areas may therefore produce incomplete estimates of a protected area's effectiveness if location bias remains unaccounted for (Joppa and Pfaff 2009). Novel statistical approaches based on matching statistics reduce bias by identifying and comparing pairs of observation points inside and outside the protected area that are most similar to each other based on a list of covariates (Andam et al. 2010). To our knowledge, however, no study has so far combined remote sensing based assessments of post-Soviet LULCC and matching statistics analyses to assess protected area effectiveness anywhere in the former Soviet Union.

There are very few places in the world where LULCC following a socio-economic and institutional shock has been as widespread and rapid as in Russia. While Russia has an extensive and long-established protected area network, the collapse of the Soviet Union gives rise to substantial concerns about the effectiveness of this network (Brandt 1992). Here, our goal was to quantify post-Soviet LULCC and to assess the effectiveness of two long-established strictly protected areas (zapovedniks) in a region representative for those with LULCC in European Russia: Oksky State Nature Reserve and Mordovsky State Nature Reserve. We analyzed a time series of Landsat images covering the time period between 1984 and 2010 across three Landsat footprints to quantify forest change and farmland abandonment in the post-Soviet period. As a measure of protected area effectiveness, we compared forest disturbance rates inside and outside the protected areas based on matching statistics. Specifically, we had three objectives:

1 to assess the rates and spatial patterns of forest disturbances and subsequent reforestation within and outside the protected areas;

2 to assess the rates and spatial patterns of farmland abandonment and subsequent reforestation; and

3 to evaluate the reserves' effectiveness in preventing loss of forest habitats due to logging and how this relates to the reserves' surrounding land use in European Russia.

2 Methods

2.1 Study area

Our study area was located in European Russia and covered more than 67,000 km² within Ryazan Oblast and Mordovia Republic, about 200 km Southeast of Moscow (Figure II-1). Altitude varies from about 100 to 300 m. The climate is temperate-continental, with warm summers (mean July 19.8°C) and cold winters (mean February -11.6°C), and mean annual precipitation of 534 mm (Priklonsky and Tichomirov 1989). The region is part of the temperate broadleaf and mixed forest biome and located at the junction of two ecoregions: the sarmatic mixed forest with boreal forests dominated by spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) as well as mixed temperate (with oak, *Quercus robur*) forests in the North, and the East European forest steppe with a mosaic of deciduous forests of lime (*Tilia cordata*) and oak and steppe vegetation in the South (Olson et al. 2001).

Ryazan Oblast and the Republic of Mordovia are characterized by low population densities (29.1 and 31.6 persons per km² in 2010, respectively, Heaney 2011) and decreasing population size, with a net loss of 14.6 % and 14.2 % from 1989 to 2009, respectively (ROSSTAT 2002, 2010). This period was also characterized by strong rural depopulation with a net loss of 27.5 % from 1989 to 2010 (472,000 to 342,000 residents) in Ryazan

Oblast and a similar decline in Mordovia Republic (- 23.2 %, 423,000 to 325,000 residents, ROSSTAT 2002; Heaney 2011). At the same time, relatively moderate urban population loss occurred (-7.6 %, 876,000 to 809,000 urban dwellers, in Ryazan Oblast and -7.2 %, 541,000 to 502,000 urban dwellers, in Mordovia Republic, ROSSTAT 2002; Heaney 2011). With a long history of land use, the study region is representative for European Russia, where heavy forest use started in the 18th and 19th century due to increased timber demand during industrialization. Forest management in Soviet times was characterized by overexploitation and forest resource degradation due to industrial pollution, and heavy exploration of the Asian part of Russia (Krankina and Dixon 1992). At the time of the collapse of the Soviet Union, however, the Europe-Ural geographic region was still the centre of timber production and consumption (Krankina and Dixon 1992). The forests in the northern part of the study region mainly occur on marginal soils, and in the Northwest, the Meshchera Lowlands form a flat and marshy forested area that had been drained during the 20th century to enable peat extraction (Potapov et al. 2011). In the southern part, large-scale farming with row-crop agriculture is dominating, with livestock farming on the pastures in the floodplain areas of the Oka River and its tributaries. Because humans have exploited forests in European Russia for centuries, the present extent of intact forests in European Russia is small (Yaroshenko et al. 2001; Aksenov et al. 2002). This translates into a high priority to protect the remaining old-growth and close-to-nature forests, especially in the comparatively densely populated areas around Moscow.

Two strictly protected areas are located in the study region: Oksky State Nature Reserve and Mordovsky State Nature Reserve (Figure II-1). These zapovedniks were established in 1935 and 1936, respectively, and are characterized by intensive historical and current land use in their surroundings. Oksky State Nature Reserve was originally founded to protect the Russian desman (*Desmana moschata*) (Priklonsky and Tichomirov 1989) and is located in the Meshchera Lowlands in the floodplain of the Pra River, a swampy area with poor, sandy soils that is part of a wetland of international importance (Oka & Pra River Floodplains, 1994, Ramsar Convention of Wetlands). The protected area covers about 77,000 ha of coniferous and mixed forests, wetlands, and meadows, and was designated as a biosphere reserve in 1978, with three protection zones of gradually differing intensities of permitted land use. The core zone (22,600 ha) equals the area of the zapovednik before 1989 and has the highest possible protection status (IUCN Ia). In the transition zone (33,100 ha; added in 1989), non-timber forest product use (e.g., collection of berries, mushrooms, and medicinal plants) is allowed. The buffer zone of 22,000 ha completes the biosphere reserve; there are few restrictions on land use in that zone (V. P. Ivanchev 2009, 2011, personal communication). Mordovsky State Nature Reserve is located about 130 km East of the Oksky State Nature Reserve over the area that had been protected by the Sarov monastery since the 18th century. Established to protect old-growth forests of the taiga zone (Tereshkin et al. 1989), it contains only one protection zone (IUCN Ia) encompassing 64,900 ha. Dominant land cover is coniferous and mixed forest, including some old-growth forest remnants (Tereshkin et al. 1989). The northern part of Mordovsky State Nature Reserve (22,400 ha) is a closed area and controlled by the city of Sarov, a Russian center for nuclear research.

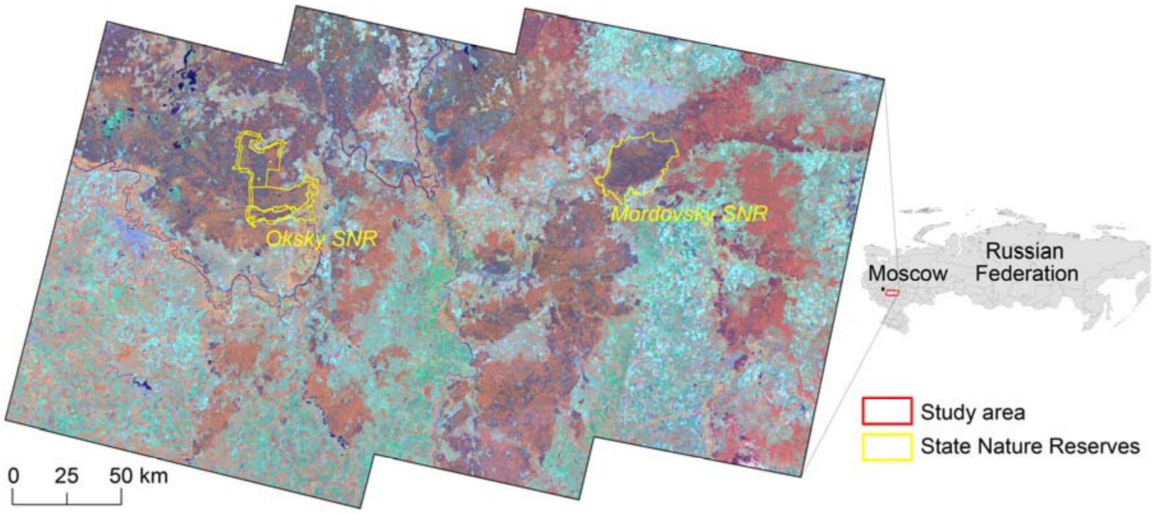

Figure II-1: Study area in European Russia with Oksky and Mordovsky State Nature Reserves (Landsat footprints path/row (acquisition date): 176/22 (2007-05-31), 175/22 (2000-05-28), and 174/22 (2007-08-21), in band combination 4/5/3, i.e., false colour). Photosynthetically active vegetation is shown in reddish colours (e.g., different forest types or cultivated agricultural land).

2.2 Satellite images and ancillary data

We acquired a time series of 38 summer Landsat TM/ETM+ scenes covering three footprints of path/row 176/22, 175/22, and 174/22 for the years 1984-2010 (Table II-1). Image availability was mainly limited by cloud coverage. Maximum cloud cover in the selected images was 22 %. We excluded the thermal bands from further analysis due to their coarser resolution. We did not apply any radiometric normalization since the support vector machines (SVM) classifier should not be impaired by radiometric differences among images (Huang et al. 2002), and the forest disturbance index includes an image-based normalization procedure (Healey et al. 2005). We co-registered the nine images from the European Space Agency to the terrain-corrected L1T imagery from the United States Geological Survey (USGS) with a maximum positional error of <0.5 pixels (mean RMSE

0.347). To remove clouds and cloud shadows, we manually digitized cloud masks on screen. We used an existing LULCC map for the Landsat footprint 176/22 for the time period 1988 to 2009 (Prishchepov et al. 2012a) as well as georeferenced topographic maps (1:100,000, VTU GSh 1989). Furthermore, we used vector boundaries of the two protected areas (OSNR 2009; IUCN and UNEP-WCMC 2011).

Table II-1: Landsat imagery acquired for the years 1984-2010 (paths 176, 175, and 174; row 22).

Year	Path 176	Path 175	Path 174	Sensor
1984		25 June	06 September	TM-5, TM-5
1986	08 September	15 June		TM-5, TM-5
1987			11 June	TM-5
1988	21 July		23 July	TM-4, TM-4
1989	17 August	18 August		TM-5, TM-4
1991	24 September	03 October		TM-5, TM-5
1992	06 June			TM-5
1993		02 June		TM-5
1994	16 September			TM-5
1995	15 June	08 June	19 July	TM-5, TM-5, TM-5
1996		12 July		TM-5
1997	19 May			TM-5
1998	07 June		09 June	TM-5, TM-5
1999	06 September			ETM+
2000	14 July	28 May		TM-5, ETM+
2002	09 May	11 June	30 July	ETM+, TM-5, ETM+
2004			28 August	TM-5
2006	01 September	08 July	19 September	TM-5, TM-5, TM-5
2007	31 May	12 August	21 August	TM-5, TM-5, TM-5
2009	09 September	16 July		TM-5, TM-5
2010	24 June		26 June	TM-5, TM-5

Several layers of biophysical and socio-economic variables were generated as covariates in the statistical analyses (see section 2.4). First, the distance to forest edge, second, the distance to the nearest city (VTU GSh 1989), third, the distance to the nearest road (VTU GSh 1989), fourth, elevation (USGS Global Digital Elevation Model), fifth, slope (NOAA Global Land 1-km Base Elevation Project), and last, percent of evergreen trees versus deciduous (MODIS Land Cover, MCD12Q1, Land Cover Type 1 (2005): IGBP global vegetation classification scheme). Distances were calculated as Euclidean distances.

2.3 Change detection

Our mapping of land-use and land-cover changes in the study region incorporated two steps: (a) a SVM classification to map forestland and farmland abandonment, and (b) a trajectory analysis to determine forest disturbances (Figure II-2). Here, we define forest disturbance as the complete removal of tree cover in a Landsat pixel at a certain time, regardless of the cause, i.e., including both human-induced and natural forest disturbance.

First, we stacked images centered around 1988 and 2010 to derive a forestland mask (to be used in the trajectory analysis) and to map farmland abandonment. Detecting farmland abandonment is challenging due to the spectral complexity of this class (e.g., spectral ambiguities between intermediate crops as well as between fallow land and particular crops and grassland, young forest, and the great spectral variability in crop types before abandonment and post-abandonment succession vegetation). Capturing these phenological differences (e.g., varying stages of maturing and senescent crops in active agricultural land or low variation in abandoned fields with shrub encroachment) is important to separate active from abandoned agriculture (Kuemmerle et al. 2008; Baumann et al. 2011; Prishchepov et al. 2012b). Thus, we included two satellite images for each time step ideally acquired at different times in the growing season and in different years (path/row 176/22: 1988-07-21, 1988-08-22, 2007-05-31, and 2009-09-09; path/row 175/22: 1986-06-15, 1989-08-18, 2006-07-08, and 2009-07-16; path/row 174/22: 1987-06-11, 1988-07-23, 2007-08-21, and 2010-06-26).

We used support vector machines (SVM) as our classifier, a machine learning algorithm that is well suited to map spectrally complex classes (e.g., multimodal), which are common for change classifications (Huang et al. 2002). The basic approach of an SVM classifier is to identify a hyperplane that optimally separates two classes in the feature space. SVM frequently outperform other non-parametric and parametric classifiers (Foody and Mathur 2004) and require few training data (Foody and Mathur 2006). SVM have been successfully applied for mapping land-use change in general and farmland abandonment in particular (Kuemmerle et al. 2008; Hostert et al. 2011; Prishchepov et al. 2012a).

We classified the stack of four images for each footprint into five LULCC classes: (1) stable agriculture, i.e., arable fields and actively managed grasslands for hay cutting and livestock grazing that were in use in both points in time; (2) abandoned agriculture, i.e., fields and pastures that were in use at the end of the 1980s, but abandoned in 2010, including areas that had reverted to forests; (3) unmanaged grasslands and riparian trees;

(4) forest, i.e., forest of different types as well as sites of forest disturbance and post-disturbance succession, but not abandoned areas; and (5) other including water, settlements, and roads. Training data were comprised of randomly distributed points (100-300 per class) that we labelled based on field visits (e.g., for farmland abandonment), very high resolution data provided via Google Earth, topographic maps (e.g., for elements of the ‘other’ class), and the Landsat satellite images themselves. Additionally, we digitized training points to bolster sample sizes for small and spectrally complex LULCC classes, such as disturbed forest areas (small) and farmland abandonment (spectrally complex).

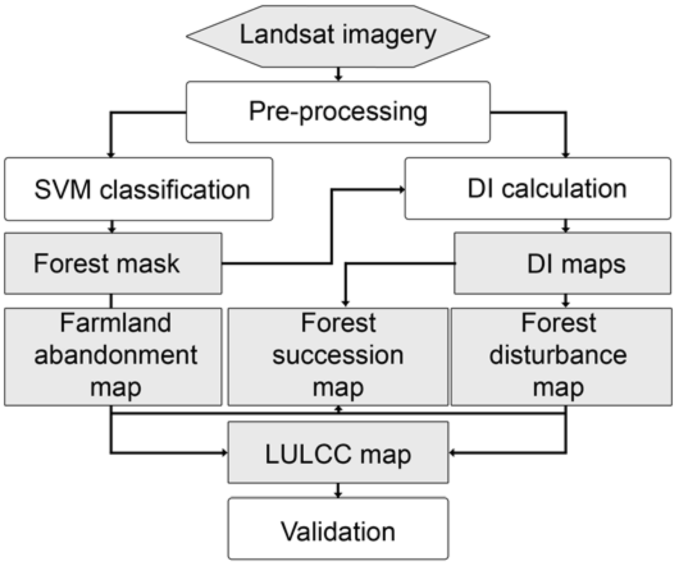

Figure II-2: Work flow of land-use and land-cover change (LULCC) detection (SVM = support vector machines, DI = disturbance index).

Second, we applied a trajectory-based forest disturbance detection to map forest-cover change between 1984 and 2010. For each pixel of all images in our Landsat time series, we calculated the forest disturbance index (DI), which is a linear transformation of the normalized Tasseled Cap (TC) indices (Healey et al. 2005). The DI assumes that disturbed forest is characterized by high brightness, low greenness, and low wetness. First, the Tasseled Cap indices were normalized to a mean of zero and standard deviation of one using a representative forest reference population (i.e., all forest areas that remained undisturbed across time). Second, the normalized Tasseled Cap indices were linearly combined as: DI = nBr – (nGr + nWe) where n refers to normalized Tasseled Cap (TC) brightness (Br), TC greenness (Gr), and TC wetness (We) components. In other words, normalized brightness values are reduced by the sum of the normalized greenness and wetness (Healey et al. 2005).

In a given DI map, a DI value of 0 specifies areas that are close to the mean spectral characteristics of forests and therefore likely denotes forest. Conversely, large DI values represent spectral dissimilarity to the forest reference population (e.g., a DI = 2 refers to a spectral dissimilarity of two standard deviations to the reference population), thus likely denoting non-forest areas (or a forest disturbance when analyzed in a temporal trajectory). Mapping forest disturbances requires setting two user-defined thresholds (Healey et al. 2005). A first threshold indicates the upper range of DI values of areas considered closed-canopy forests. The second DI threshold denotes DI values above which an area can be considered a non-forest (i.e., disturbed) area. Values between both thresholds characterize various stages of degraded or regrowing forest (Healey et al. 2005). We defined the two DI thresholds based on the DI statistics of areas with known disturbances in different forest types as well as undisturbed forest (based on field visits and visual digitizing from the Landsat images themselves) as well as experience from a range of previous applications of the concept in temperate forests (e.g., Healey et al. 2005; Kuemmerle et al. 2007) (Table II-S1). In our study area, DI values lower than 2 represented intact, undisturbed forest, whereas forest disturbances were characterized by DI values larger than 4 to larger than 10 (depending on the image). This variation was caused by differences in the phenological and weather conditions of our imagery over time, both affecting the Tasseled Cap indices. Another factor contributing to the variability in upper DI thresholds was the time interval between subsequent images in the time series that influenced the degree of post-disturbance forest succession on disturbance sites. Based on the two thresholds, we flagged each pixel in each image of our time series as either undisturbed or disturbed forest.

Once a time series of disturbance images was available, we carried out a trajectory analysis to remove false detections. When analyzing several DI maps in a temporal trajectory, an increasing DI value over time towards non-forest indicates forest disturbance, and a decreasing DI value over time characterizes forest recovery. Starting with a cloud-free image, we therefore identified those disturbance pixels that showed both a DI value lower than 2 in the first year and a value greater than the second threshold in the respective year of forest disturbance (Figure II-3).

To map forest disturbance, we used a minimum mapping unit of four Landsat pixels, i.e., 0.36 ha, which was chosen to sieve speckle and to remove pseudo-change pixels due to remaining positional inaccuracy of some images. We then visually checked all detected forest disturbances and evaluated whether a disturbance was caused by logging (e.g., regular shaped, mainly rectangular form, mostly small) or fire (e.g., burn scar clearly visible in false-colour combinations, irregularly shaped, often large), also using additional Landsat images, which were not included in the time series due to high cloud coverage. We labelled post-fire logging (i.e., clear-cutting on burned forest areas up to five years after the fire event, Schroeder et al. 2012) as logging since salvage logging represents forest management. This yielded annual forest disturbance maps for the period 1984-2010, where each forest disturbance was either labelled as logging or fire. We then calculated annual forest disturbance rates by dividing the area disturbed in a given year by the total forest area in 1984/86 (i.e., the forest mask from our initial SVM classification adjusted to the forest area in 1984/86 using the earliest images of our time series, path/row 176/22: 1986-09-08, path/row 175/22: 1984-06-25, and path/row 174/22: 1984-09-06). For years without image in our time series (Table II-1), we evenly distributed the disturbance area mapped in the next year when an image was available across the observation year plus all preceding years in that gap period.

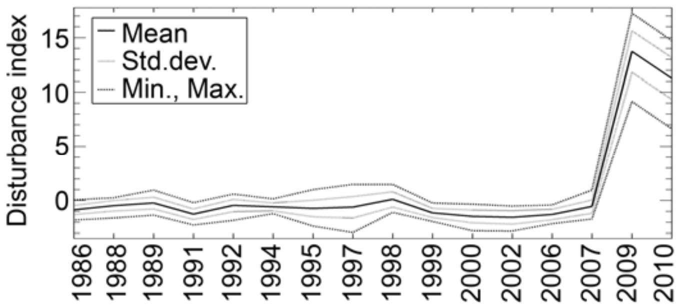

Figure II-3: Trajectory of forest disturbance index values across the available Landsat imagery (1986-2010, see Table II-1) for digitized site (34 pixels) of a forest disturbance in 2009.

We then combined the land-cover change map and the forest disturbance map to assess forest succession both on abandoned farmland and in previously disturbed forests. Forest succession was mapped based on the similarity of a non-forest pixel to the mean spectral characteristics of forests (i.e., the DI value image). Specifically, we labelled abandoned areas as forests and disturbed areas as recovered once the DI values on these areas showed a DI value within two standard deviations around the mean DI of forest spectral characteristics ($-2 < DI < 2$).

We validated our results based on a stratified random sample of points that was independent from those used for training. We used 300 points for each of the LULCC classes stable agriculture, abandoned agriculture, unmanaged grasslands and riparian trees, forest, and other, and 50 points for each of the 20 forest disturbance years (1986-2010). To minimize spatial autocorrelation, we used a minimum distance of 1 km between points. We labelled points based on very high-resolution satellite images (available in Google Earth), the Landsat images themselves (Kuemmerle et al. 2009; Cohen et al. 2010; Zhu et al. 2012) and field visits. We calculated an error matrix, calculated user's, producer's, and overall accuracies, and corrected for sampling bias in the error estimates (Foody 2002; Olofsson et al. 2013). We also calculated true area estimates as well as the 95% confidence intervals around these estimates based on the uncertainty in our LULCC map (Card 1982) grounds.

2.4 Evaluating the effectiveness of Oksky and Mordovsky State Nature Reserves

To assess the effectiveness of the two strictly protected areas in preventing forest disturbances inside them during post-Soviet times, we first summarized forest disturbance both within the nature reserves (in case of Oksky State Nature Reserve separately for all protection zones) and in their surroundings. The latter was done using four buffers of 0-5, 5-10, 10-15, and 15-20 km from the outer boundary of the protected areas (Figure II-4). This represents the classic approach to measuring protected area effectiveness (Curran et al. 2004; DeFries et al. 2010).

Second, we evaluated the protected area effectiveness by using matching statistics to control for the non-random allocation of protected areas and the potential displacement of land uses to surrounding areas, e.g., forest disturbance spillovers to adjacent forests (Andam et al. 2008; Ferraro et al. 2011; Wendland et al. 2011). For our matching statistics, we took a random sample of 1 % of forested pixels within the two protected areas and four times this number of forested pixels outside of the nature reserves. We then assigned each pixel a propensity score measuring the likelihood that the pixel was protected. A propensity score summarizes multiple characteristics into a single-index variable and is estimated using a logit model (Becker and Ichino 2002). In total, only very few points within the forest areas (<1 % for all sample sizes tested) were affected by fires. Forest fire is therefore negligible in our matching analyses and the observed effects of forest disturbances on protected areas effectiveness can be solely attributed to logging (including salvage logging). We included biophysical and socio-economic characteristics expected to impact the probability of protection in the propensity score. The distance to the nearest road served as a proxy for the impact of infrastructure, the distances to the nearest city and to Moscow served as a proxy for the importance of market access and outside timber demand (i.e., Moscow) (Mueller and Munroe 2008; Wendland et al. 2011). Elevation and slope characterized the roughness of the terrain, thereby possibly affecting the effort of human-induced forest disturbance. The distance to forest edge is expected to indicate the impact of prior human-caused disturbance, and the percent of evergreen (versus deciduous) trees related to a potential influence of the forest type on the disturbance regime.

Observations within the protected areas were then matched to pixels outside based on the minimum linear distance between propensity score values. We dropped protected area pixels with a propensity score higher than the maximum or less than the minimum propensity scores of observations outside of the protected areas. Such "common support" ensures good matches (Caliendo and Kopeinig 2008). The average difference in land-use outcomes was then calculated as the difference in means between these matched populations. However, matching does not always eliminate all differences between pixels within and outside of protected areas, and we checked for remaining differences by comparing the covariate balance in the matched sample. Covariate balance was calculated as the normalized difference in means: $\overline{X_1} - \overline{X_2} / \sqrt{\sigma_1^2 + \sigma_2^2}$, where $\overline{X}$ is the mean covariate value, σ^2 the variance, and the subscripts designate areas within (1) and outside (2) of protected areas.

In general, a normalized difference in means greater than 0.25 is "large" (Imbens and Rubin Forthcoming). When matching was incomplete, regressions of the matched sample were used to further reduce bias (Imbens and Wooldridge 2009). We found that matching did not lead to complete covariate balance in our analysis; therefore, we performed a logistic regression analysis using the matched sample and controlling for each of the covariates listed above. The marginal effect (i.e., the derivative of the prediction function) of the protected area status on forest disturbance is equivalent to the effectiveness of the protected area because it describes the increase in likelihood of our outcome and thus reveals the mean effect of a protected area on forest disturbance. To enable a comparison of the effectiveness of Oksky and Mordovsky State Nature Reserves despite the differences in available satellite imagery for the various Landsat footprints across time (Table II-1), we generated forest/non-forest maps for five 5-year time periods, i.e., 1986-1990, 1991-1995, 1996-2000, 2001-2005, and 2006-2010 and repeated the matching statistics for each time period.

3 Results

3.1 LULCC mapping

Our change analyses resulted in reliable maps of forest disturbance and farmland abandonment for the time period of 1984 to 2010. The area-adjusted overall accuracy of the LULCC map, containing 25 classes, was 71.25 % (Table II-2 and Table II-3). The most widespread classes stable agriculture, abandoned agriculture, and stable forest, were all mapped with moderate to high user's (all classes ≥59.06 %) and producer's (≥75.95 %) accuracies. The forest disturbance classes had on average high user's accuracies (mean = 97.19 %), but lower producer's accuracies (mean = 15.41 %; Table II-3).

Table II-2: Confusion matrix for the merged LULCC map including the detected forest disturbances (B = Background, A = Stable agriculture, AA = Abandoned agriculture, G = Grassland and riparian trees, F = Stable forest, YYYY = Forest disturbance in respective year).

LULCC map/ Refe-rence	B	A	AA	G	F	1986	1987	1988	1989	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2002	2004	2006	2007	2009	2010	Total
B	162	9	7	10																						188
A	11	161	17	17																						206
AA	2	27	146	16	1																					192
G	6	10	18	148	2																					184
F	7	1	7	16	176	2	7	3	7	3	2	4	3	3	6	9	6	7	6	6	6	4	2	3	2	298
1986					1	35																				36
1987							41																			41
1988								45																		45
1989	2			3					31					1												37
1991	1									30																31
1992											45															45
1993												41														41
1994													42													42
1995	1													42												43
1996					2										39											41

1997					3											34										37
1998	1				1												39						1			42
1999																		43								43
2000																			39							39
2002				1																43						44
2004				1																	42					43
2006																						45				45
2007				1																			39			40
2009	2																							44		46
2010																									47	47
Total	195	208	195	213	186	37	48	48	38	33	47	45	45	46	45	43	45	50	45	49	48	49	42	47	49	1896

Table II-3: Area-adjusted overall accuracy (OA), producer's (PA) and user's (UA) accuracies of the merged LULCC map including the detected forest disturbances (B = Background, A = Stable agriculture, AA = Abandoned agriculture, G = Grassland and riparian trees, F = Stable forest, YYYY = Forest disturbance in respective year).

	PA (%)	UA (%)
B	32.52	86.17
A	86.26	78.16
AA	75.95	76.04
G	61.89	80.43
F	98.98	59.06
1986	18.44	97.22
1987	20.37	100.00
1988	30.43	100.00
1989	8.68	83.78
1991	22.91	96.77
1992	10.37	100.00
1993	6.14	100.00
1994	10.71	100.00
1995	43.90	97.67
1996	1.53	95.12
1997	2.47	91.89
1998	8.22	92.86
1999	2.25	100.00
2000	7.99	100.00
2002	15.53	97.73
2004	3.98	97.67
2006	32.34	100.00
2007	18.52	97.50
2009	15.85	95.65
2010	27.50	100.00
OA (%) = 71.25		

In 2010, the study region was composed of a heterogeneous landscape characterized by 46.07 % agricultural land (active and abandoned farmland), 40.20 % forest area, 12.06 % grasslands and riparian trees, and 1.67 % water bodies, settlements, and roads (Figure II-4).

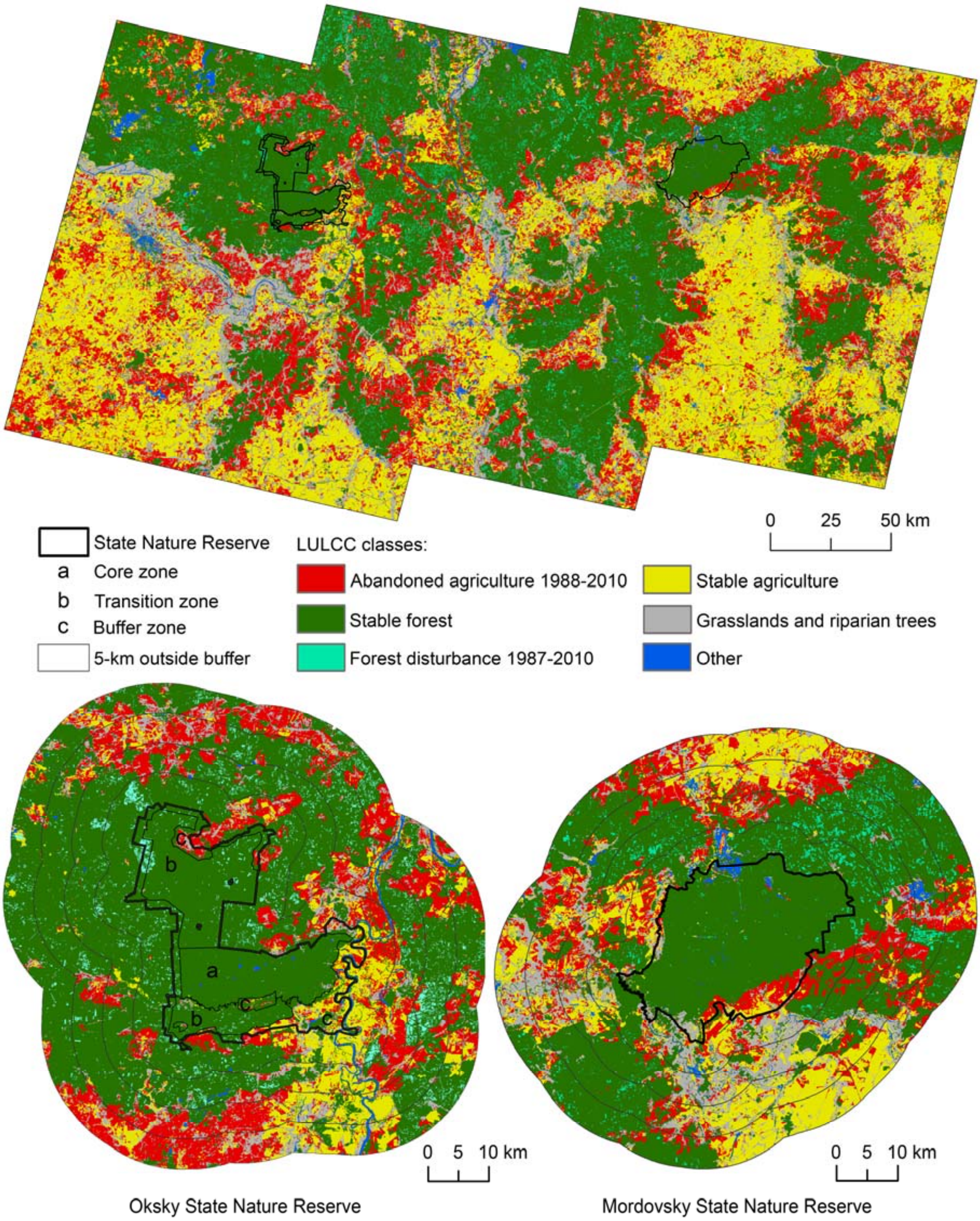

Figure II-4: Post-Soviet land-use and land-cover change (LULCC) within the study area and Oksky and Mordovsky State Nature Reserves with their surrounding ring-shaped buffers within 0-5, 5-10, 10-15, and 15-20 km of the outermost boundary of the protected areas.

Abandonment of agricultural land was widespread in the study region and occurred on 18.37 % of the total landscape in 2010, and 39.89 % of the 1988 agricultural land (1,281,331 ha arable land in 1988; Figure II-4). Most abandoned land was located in the vicinity of forests. On 9.20 % of the abandoned area (117,897 ha) forests had established by 2010.

In our study region, 5.02 % of the total forest area was disturbed between 1984 and 2010 (137,912 ha; Figure II-4). We did not find any repeated disturbances in our analyses. Annual forest disturbance rates varied from 0.13 % in the years 1996, 1997, 1999, and 2000 up to 0.49 % in the years 1985 and 1986 (mean 0.23 %, standard deviation 0.1; Figure II-5). Our results also showed distinct temporal trends in forest disturbance rates. In the late Soviet era from 1986 to 1990, forest disturbance was highest (40,254 ha for the total period from 1986 to 1990, representing 1.44 % of the total forest area in 1984). After the collapse of the Soviet Union, the disturbance rates declined to a low-point in the 1990s (29,338 ha of disturbed forest relative to the total forest area in 1984, equalling a share of 1.05 % from 1991 to 1995, and 16,367 ha of disturbed forest equalling a share of 0.58 % from 1996 to 2000). Subsequently, forest disturbance rates increased again, but only to about half of the rates of the late-Soviet period (23,187 ha and 21,279 ha from 2001 to 2005 and 2006 to 2010, respectively, equalling a share of 0.83 % and 0.76 %, respectively). Discriminating the forest disturbances due to fire and logging (including post-fire logging) reveals that the main trend in disturbances is due to logging (Figure II-5). Burned forest areas, however, increased markedly after 1999, sharing up to 21 % in 2008 (Figure II-5). Although the accuracy of our forest disturbance classes varied over time (Table II-3), the 95 % confidence intervals of our area estimates were relatively moderate and did not suggest a bias regarding the overall trend in forest disturbance across the time period (Figure II-5).

Forest recovery on previously disturbed sites within the forest (i.e., not forest expansion on abandoned land) was also a widespread process in the study area. Our analyses suggested that forests required about 10-15 years to recover from disturbance and thus to be again classified as forest (Figure II-5). About 46.19 % of the forest that had been disturbed between 1984 and 2010 had regrown by 2010 (63,708 ha).

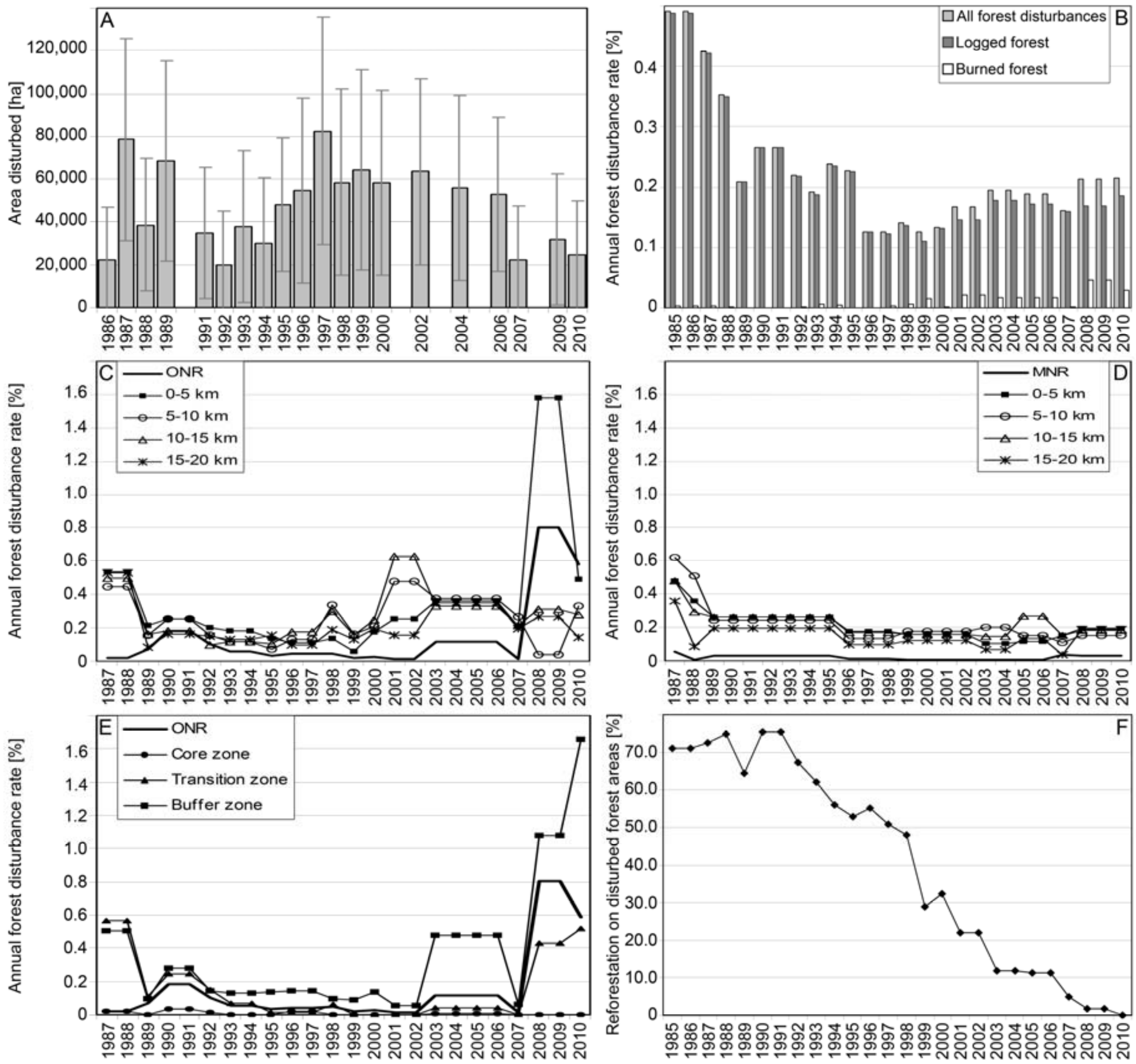

Figure II-5: (A) Annually disturbed forest area with error bars indicating the 95% confidence intervals; (B) Annual disturbance rates (all forest disturbances, logged, and burned forest) for the entire study area in per cent of the total forest area in 1984/6; (C) Annual forest disturbance rates for the protected areas of Oksky (ONR) and Mordovsky (D, MNR) State Nature Reserves and their surrounding ring-shaped buffers within 0-5, 5-10, 10-15, and 15-20 km of the outermost boundary of the protected areas; (E) Annual forest disturbance rates for the different protection zones of Oksky State Nature Reserve (ONR); (F) Reforestation on disturbed forest areas in the study region in 2010 (with year of forest disturbance).

3.2 Protected area effectiveness

Our matching statistics approach revealed that within both protected areas, Oksky and Mordovsky State Nature Reserves, forest disturbance rates were significantly lower than in their surroundings (Figure II-4). This suggests that both protected areas had a statistically significant effect on protecting forests inside them from forest disturbance.

In Oksky State Nature Reserve, forest disturbances occurred on about 1,241 ha between 1986 and 2010, equaling 1.81 % of the protected forest area (annual rate = 0.08 %). Within the core zone of the protected area, only 0.19 % of the forest area had been disturbed over that same period (41 ha), with annual forest disturbance rates never exceeding 0.03 % (Figure II-5). Within the transition zone, disturbances were more frequent and occurred on 1.57 % of the forest area in this zone between 1989 (i.e., the year of establishment) and 2010 (517 ha). Yet, within the first years after extending the protected area by the transition zone, annual disturbance rates decreased substantially from 0.56 % in 1987 and 1988 (i.e., prior to establishment) to rates below 0.10 % after 1993 within this area and remained at a low level. A sharp increase in disturbance rates due to several larger wildfires occurred after 2007, when rates exceeded 0.40 % (Figure II-5). Within the adjacent buffer zone, disturbances occurred on about 5.09 % of the total forest area (683 ha out of 13,415 ha; 1989-2010). Showing a similar pattern as in the transition zone, annual disturbance rates within the buffer zone remained below 0.15 % in the late-Soviet era and until 2001, but increased to 0.45 % by 2003 and further up to 1.66 % in 2010 (Figure II-5). Outside of Oksky State Nature Reserve, forest disturbances occurred on about 4.80 to 6.15 % of the forest area within each of the four 5-km buffer areas (1986-2010). Annual forest disturbance rates within the surroundings were always higher than within the protected area itself, except for the years after 2007, when large forest fires occurred within the transition and buffer zones of Oksky State Nature Reserve (Figure II-5). The forest disturbance trend of the surrounding area was similar to that of the entire study region, with annual disturbance rates decreasing in the 1990s and increasing after 2000. Disturbance rates after 2000 also varied more in magnitude from year to year and among the surrounding buffer areas than those before 2000.

The matching statistics analysis suggested that Oksky State Nature Reserve prevented forest disturbances inside its boundaries since the relative probability of a pixel experiencing forest disturbance within Oksky State Nature Reserve was lower compared to a pixel outside. This was true for all time periods we assessed, although among time periods, probabilities varied and increased in general (from -2.0 % in 1986-1990 to -0.3 % in 2006-2010, Table II-5). Despite the overall relatively low probability of forest disturbance in the study region (varying probability, but in general declining from 1.12 % in 1986-1990 to 0.95 % in 2006-2010, Table II-4), and although very low rates of forest disturbance occurred within Oksky State Nature Reserve, the forests in the protected area were much less disturbed than forests outside the reserve.

Regarding Mordovsky State Nature Reserve, we found similar patterns. Within the protected area, about 277 ha of forest (0.50 %) were disturbed in the period from 1986 to 2010. Annual forest disturbance rates were very low at all times (mean 0.02 %, standard deviation 0.02; Figure II-5). In the four 5-km buffers outside of Mordovsky State Nature Reserve, disturbances occurred on 3.54 to 5.21 % of the forests in the period from 1986 to 2010. Here, annual disturbance rates were about 0.50 % in the late Soviet era, decreased to <0.26 % in the 1990s, and remained below 0.20 % after 2000 (Figure II-5). All 5-km buffers outside of Mordovsky State Nature Reserve always exhibited higher annual forest disturbance rates than the protected area itself (from 0.05 times higher in the 20-km buffer in 2007 up to 89.51 times higher in the 10-km buffer in 1988).

The matching statistics again revealed the effectiveness of Mordovsky State Nature Reserve, similar to Oksky State Nature Reserve. The relative probability of a pixel experiencing forest disturbance within Mordovsky State Nature Reserve was always lower than outside, although it increased from -3.5 % in 1986-1990 to -0.1 % in 2006-2010 (Table II-5). This confirms that the protected area was effective in preventing forest disturbance inside its boundaries.

Table II-4: Matched and unmatched observations (percent (%) and number (N)) that experienced forest disturbance within Oksky State Nature Reserve (ONR), Mordovsky State Nature Reserve (MNR), and their outside areas (Controls); unmatched samples are indicating: N within the protected areas = 1 % of forested pixels within the protected areas, and N Controls = 4x 1% of forested pixels outside of protected areas; observations were removed from the sample once forest was disturbed.

	1986-1990		**1991-1995**		**1996-2000**		**2001-2005**		**2006-2010**	
	Match	**No match**	**Match**	**No match**	**Match**	**No match**	**Match**	**No match**	**Match**	**No match**
ONR (%)	0.00	0.00	2.46	2.45	0.12	0.12	0.39	0.39	0.62	0.61
Controls (%)	1.94	1.12	3.75	4.10	0.64	0.74	1.52	1.88	1.06	0.95
ONR (N)	2,220	2,292	6,862	6,903	6,716	6,734	6,711	6,726	6,610	6,700
Controls (N)	2,220	27,844	6,862	27,532	6,716	26,402	6,711	26,206	6,610	25,714
MNR (%)	0.20	0.20	2.19	2.15	0.05	0.05	0.86	0.84	0.05	0.05
Controls (%)	2.76	2.06	3.80	5.49	0.62	0.44	1.29	1.80	0.13	0.10
MNR (N)	5,869	5,881	5,763	5,869	5,649	5,743	5,570	5,740	5,530	5,692
Controls (N)	5,869	23,523	5,763	23,038	5,649	21,774	5,570	21,679	5,530	21,288

Table II-5: Relative probability (%) of an observation within Oksky State Nature Reserve (ONR) and Mordovsky State Nature Reserve (MNR) experiencing forest disturbance in comparison to being outside of the considered protected area in the respective time period (N = matched sample). A negative relative probability highlights that a forest pixel located within a protected area has a lower probability to experience forest disturbance than a forest pixel with the same characteristics outside the protected area. A forest pixel located within Oksky State Nature Reserve (ONR), for example, has a 2 % lower probability of forest disturbance in 1986-1990 than a similar forest pixel outside ONR.

	1986-1990	1991-1995	1996-2000	2001-2005	2006-2010
ONR (%)	-2.0***	-0.9***	-0.6***	-1.2***	-0.3*
ONR (N)	2,220	6,862	6,716	6,711	6,610
MNR (%)	-3.5***	-0.8**	-0.9***	-0.1	-0.1
MNR (N)	5,869	5,763	5,649	5,570	5,530

Statistically significant at: ***1% level, **5% level, *10% level

4 Discussion

4.1 Post-Soviet land-use changes

Our analyses revealed substantial and widespread LULCC in the post-Soviet era in our study region in European Russia, most importantly widespread forest disturbance due to logging as well as farmland abandonment and subsequent reforestation. Protected areas in our study region remained effective in the post-Soviet period in safeguarding their forests from human-caused disturbance. This is remarkable, considering the institutional instability and economic hardships of the transition period from state- to market-oriented economies, and stands in contrast to protected area effectiveness elsewhere. Our results therefore provide hope for conservation during turbulent times and they provide an example of how combining Landsat trajectory analyses and matching statistics can help to monitor the success of conservation.

Changes in forest cover exhibited distinct spatial and temporal patterns, particularly the initial decline of forest disturbance rates in post-Soviet times accompanied with an increase in forest cover on former agricultural land. The initial decline of disturbance rates was most likely caused by the crisis of the forestry sector during the transition of the state-planned Soviet economy to a market-driven economy, due to the slowly developing institutional framework for the forestry sector and lacking investment incentives (Torniainen and Saastamoinen 2007). Following this initial contraction, demand for timber increased again leading to rising exports after 2000, which in turn spurred logging rates (Henry and Douhovnikoff 2008; Potapov et al. 2011; Wendland et al. 2011; Baumann et al. 2012). Part of the increase in disturbance rates we observed after 2000 is also due to natural disturbances, particularly fires, which have been increasing in the study region during that time. Several larger wildfires, for example, in 2002, but especially after 2007, caused extensive forest loss and wildfires following severe droughts affected in particular the drained forested peatlands in the Meshchera Lowlands in the North of the study area. We note that while these fires were extensive, disturbances due to logging were dominating in our study area. Both types of disturbance affect forest ecosystems, yet there are considerable differences in vegetation structure, community composition, natural vegetation recovery, soil properties, and landscape fragmentation and connectivity after logging or fire disturbances (Lindenmayer and McCarthy 2002; Lindenmayer and Noss 2006). Our results of post-Soviet land-use changes confirm earlier studies in other areas of Eastern Europe. The initial decline of forest logging rates was widespread in Russia (Peterson et al. 2009). The disturbance rates for our study region were even below those in other regions of post-socialist Eastern Europe, for example, Ukraine, Slovakia, and Romania (Kuemmerle et al. 2007; Griffiths et al. 2012; Knorn et al. 2012), which is surprising given that our study region was relatively close to Moscow, Russia's major market centre. During socialism, forests were overexploited in many regions across the Soviet Union (Nijnik and van Kooten 2006), but whether the lower timber harvesting rates since 2000, which are only about half of the Soviet rate in our study region, are more sustainable, remains unclear. Old-growth forests in that region of Russia are scarce (Yaroshenko et al. 2001). Timber extraction is still a main threat to Russian forest habitats and protected areas (Ervin 2003), and illegal logging continues (Tyrlyshkin et al. 2003; EEA 2007).

The abandonment of farmland in post-Soviet time was the most widespread land-use change in our study area. The main underlying causes of abandonment in Russia were the breakdown of Russia's agricultural sector due to disappearing, formerly guaranteed markets for agricultural products and timber within the Soviet sphere of influence, price liberalization of agricultural inputs (e.g., fertilizer, machinery) and outputs (e.g., agricultural products) due to the deregulation of fixed market prices, rising international competition, a shortage of labour in Russia's rural areas due to outmigration into urban areas accompanied with low birth rates and a decreasing life expectancy during the 1990s, and the post-Soviet reforms in land ownership and market structures (Brooks and Gardner 2004; Ioffe et al. 2004; Lerman et al. 2004; Prishchepov et al. 2012a). The high rate of abandonment in our study area was similar to abandonment rates in other regions in European Russia (Prishchepov et al. 2012a), and ranks among the highest in Eastern Europe (Kuemmerle et al. 2008; Baumann et al. 2011; Prishchepov et al. 2012a).

Recultivation of agricultural land has increased in Russia since 2005, and a strong interest in Russia's currently unused land for producing both food and bioenergy is arising (Vuichard et al. 2008). Yet, this was not the case in our region, where abandonment continued to increase in the second post-Soviet decade and the rate of recultivation of abandoned farmland was generally low (1.5 % in Ryazan Oblast, 2000-2010, Prishchepov et al. 2012a). Abandoned farmland typically transitions to grassland and then to forest via several successional stages. In our study area, many abandoned farmlands (>10.0 %) had already reverted to forests and it is unlikely that these lands, particularly those on poor soils, will be put back into production due to limited interest in such land and high recultivation costs (Larsson and Nilsson 2005; Schierhorn et al. 2012). Forest succession on abandoned marginal farmland will likely continue in the near future, affecting landscape configuration and forest connectivity. Currently, these post-agricultural forests are not managed by the forest service. Although the future of abandoned farmlands remains unclear (some recultivation has recently been taking place on fertile land in our study region), an appropriate management of abandoned land would lower the risk of exacerbating fires originating from these lands with unmanaged forest succession that may impact both biodiversity and ecosystem services (Navarro and Pereira 2012).

Although our change detection approach yielded reliable maps of post-Soviet LULCC for our study area in European Russia, some uncertainties remain. First, our forest disturbance estimates are likely conservative due to the minimum mapping unit we applied and the relatively high disturbance index thresholds we used, which were selected to minimise errors of commission of the forest disturbance class (Lu et al. 2004). Second, while we visually classified natural and fire disturbances to assess general trends in these disturbance causes, we did not identify the causes of disturbance in our change detection. If training data on different types of disturbances would become available, a more comprehensive assessment to discriminate natural and human-induced forest disturbances could be performed (Schroeder et al. 2011). Third, we chose a conservative approach to assess succession on abandoned farmland as well as forest recovery of disturbance sites via labelling only those pixels as reforested that were spectrally similar to mature forest. This may have resulted in an underestimation of forest expansion and forest recovery as early-successional forest often lacks typical shadow effects in mature forests and is composed of different tree species (e.g., *Betula* or *Pinus*) with brighter reflectance than mature forests (i.e., leading to higher DI values). Fourth, some of our forest disturbance estimates had low producer's accuracy. A visual assessment suggested that wrongly classified validation points were mainly due to remaining positional inaccuracy among the USGS L1T and the images from other sources. Although individual positional accuracy was high (<0.5 pixels for all images), co-registration errors caused the misclassification of a few points, in particular, at the edge of forest disturbances (Zhu et al. 2012), which often was classified as undisturbed forest. As these omission errors were found in relatively small classes, the area weighting we carried out penalized such misclassifications strongly. It is important to note though that these accuracies have no significance for any of our conclusions since they mainly represent misregistration errors which are likely not biased towards a certain time period or area within our study region. Furthermore, we incorporated the uncertainty in our analyses by calculating true area estimates for all classes as well as the 95% confidence intervals around these estimates. We also note that our error estimates and change rates are well in line with other studies (e.g., Potapov et al. 2011; Baumann et al. 2012; Prishchepov et al. 2012a).

Changes in land use and land cover occurred in our study area throughout the entire period of 1984 to 2010, with forest disturbances and farmland abandonment likely affecting habitat availability and fragmentation for a variety of species. Only time will tell, however, what the exact effects of current trends of post-Soviet LULCC at the species level are, and whether these trends will continue into the future. Generally, current LULCC trends may pose both threats and opportunities. For example, continued abandonment of farmland could lead to widespread forest expansion, benefitting those species thriving in natural ecosystems (Kuemmerle et al. 2010; Orlowski 2010). Conversely, farmland abandonment may threaten agrobiodiversity (Fischer et al. 2012), as highlighted in the Carpathians, for example, where abandonment threatens subalpine grasslands (Baur et al. 2006). Moreover, accelerating forest logging rates and recultivation of fallow land (with intensified agricultural use) in the surroundings of the nature reserves may pose new challenges for conservation and protected area effectiveness. Further research is needed to assess future threats and opportunities for conservation in the temperate broadleaf and mixed forest biome, one of the currently most threatened biomes in the world (Hoekstra et al. 2005).

4.2 Effectiveness of Oksky and Mordovsky State Nature Reserves

The two strictly protected areas, Oksky and Mordovsky State Nature Reserves, were overall effective in limiting logging within their boundaries, despite the rapid institutional changes after the breakdown of the Soviet Union. This is surprisingly, given that some protected areas in Russia were struggling after the breakdown of the Soviet Union (Colwell et al. 1997; Fiorino and Ostergren 2012) and nature reserves in other post-socialist countries, for example, the Ukraine (Kuemmerle et al. 2007) or Romania (Ioja et al. 2010; Knorn et al. 2012), were less effective in preventing threats to habitats and wildlife. The reasons for this remain unclear, but potential explanations are the long time period that both protected areas existed, the relative closeness of both protected areas to Moscow, the fact that they are federally managed by the Ministry of Natural Resources and Environment of the Russian Federation, the comparatively numerous and well-trained protected area staff, or the reason that funding may have declined less for these protected areas than for others in Russia (e.g., Oksky State Nature Reserve is a major centre of crane and European bison breeding and participates in many international projects). Further explanations are the relatively low population density in the study region, the ease of access to similar forest resources outside the protected areas, as well as the reduced pressure on the forests due to the generally decreasing forest disturbance rates in post-Soviet times.

Over time, the effectiveness of our two protected areas on curbing forest disturbance declined, but this was largely because the probability of forest disturbance in their surroundings declined in the post-Soviet period as well (Wendland et al. 2011). Thus, in terms of forest disturbance, the surroundings of the protected areas became more similar to the protected areas themselves (Table II-4 and Table II-5). Our results also highlighted the lagged effect that the establishment of protected areas can have in terms of effectiveness. We detected only very small forest disturbances within the core zone of Oksky State Nature Reserve during 1986 to 2010, but most forest disturbances occurred in the transition and boundary zones, especially in the years immediately after the collapse of the Soviet Union due to human-induced forest clearances. Although these zones officially had been part of Oksky State Nature Reserve since 1989, the transition zone was not fully implemented until 1995, and this is reflected in the higher disturbance rates in our results. Mordovsky State Nature Reserve has also limited forest disturbance within its boundaries. Most disturbances were detected within the closed zone controlled by the city of Sarov; however, the remaining area that was managed by the protected area staff was effective in restricting forest disturbances.

Though the causes of natural and human-induced disturbances are different, there are linkages between the two disturbance types in our study area. Importantly, we found salvage logging to occur after forest fires. For example, fire events in the buffer zone of Oksky State Nature Reserve triggered forest management and our results showed an increasing trend in fire events since 2000. This could have resulted in an increase in salvage logging within the protected areas and their surroundings.

Our analyses also highlighted that post-Soviet land-use change fundamentally restructured the surroundings of protected areas and thus, was impacting the "zone of interaction" the protected areas are embedded in. Although we detected post-Soviet LULCC such as forest disturbances and farmland abandonment (e.g., the abandonment of meadows that were used for hay cutting in Soviet times within the buffer zone of Oksky State Nature Reserve, V. P. Ivanchev 2009, 2011, personal communication) within the protected areas, LULCC was far more extensive in their surroundings. While these LULCC trends likely affect landscape configuration, further research is necessary to quantify these changes. Forest fragmentation is promoted by forest disturbances and, at the same time, by the large-scale forest succession on abandoned farmland that, even in the vicinity of the protected areas, provides the opportunity to increase forest cover and to establish novel connections between protected and unprotected species habitats.

Both methods of effectiveness estimation that we applied, the descriptive inside-outside comparison and the matching comparison, yielded relatively similar results. Yet, simple buffers, the traditional method to estimate protected area effectiveness, would not have allowed for the detailed picture provided by the matching statistics (e.g., quantification of the effect of protection, assessment of changes in effectiveness over time).

5 Conclusion and Outlook

The rapid institutional and socio-economic changes following the breakdown of the Soviet Union in 1991 triggered a drastic episode of land-use and land-cover change in our study area in European Russia. Using a time series of Landsat TM/ETM+ images, we found strong changes in logging regimes as well as widespread farmland abandonment with extensive forest succession, which likely were triggered by the fundamental socio-economic and institutional transformations. The post-Soviet period was also characterized by institutional decay, diminishing funding, and a lower level of control and this brought about substantial challenges for nature conservation in Russia. Here, we showed that despite these challenges the two strictly protected areas we assessed, Oksky and Mordovsky State Nature Reserves, remained relatively effective in safeguarding their territory from logging during the period from 1987 to 2010. This confirms that these protected areas are not "paper parks" (Bruner et al. 2001). Even during the turbulent years after the breakdown of the Soviet Union, these protected areas had a measurable effect, highlighting the importance of protection efforts. Our results thus also contribute to the wider discussion of what determines the success of protected areas providing an encouraging example that protection can work in regions of the world that are undergoing socio-economic or institutional shocks. Rapid LULCC, however, occurred within the "zone of interaction" (DeFries et al. 2010) of both nature reserves, restructuring the wider landscapes the protected areas are embedded in.

For the future, recent LULCC trends may pose both threats and opportunities for nature conservation. Threats include continued or increasing logging resulting in increasing habitat fragmentation, the spread of fires from abandoned farmland where forests are unmanaged, or recultivation of currently unused lands, whereas opportunities could rise where forest expansion on former farmland increases habitat availability and connectivity. Predicting socio-economic shocks such as the breakdown of the Soviet Union is difficult or impossible and one reason for the wide range of plausible outcomes in future biodiversity scenarios (Pereira et al. 2010). This emphasizes the need for continued monitoring of protected areas within the larger landscape they are embedded in, and combining remote sensing with matching statistics is a promising avenue for doing so.

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Supporting Information

Table II-S1: Forest disturbance index (DI) statistics of digitized plots (polygons) of known forest disturbance sites (control areas) for the respective year (YYYYMMDD) and footprint (Std.dev. = standard deviation, # = amount).

Footprint	Image	Mean DI	Std. dev.	# of polygons
174/22	19870611	10.46	5.49	101
	19880723	11.54	5.41	101
	19950719	6.30	4.03	101
	19980609	11.51	5.99	101
	20020730	10.25	4.97	101
	20040828	8.64	4.92	101
	20060919	7.02	5.11	108
	20070821	14.17	6.72	92
	20100626	15.44	9.01	101
175/22	19860615	9.35	5.97	30
	19890818	6.30	6.27	30
	19911003	6.59	6.68	30
	19930302	12.08	5.88	29
	19950608	11.32	5.01	33
	19960712	6.51	4.37	31
	20000528	16.09	5.40	35
	20020611	13.34	4.79	30
	20060708	10.84	2.79	28
	20070812	14.05	3.35	30
	20090716	12.88	4.08	30
176/22	19910924	8.91	4.81	130
	19920606	13.64	4.34	76
	19940916	6.98	3.20	118
	19950615	12.80	4.95	74
	19970519	16.21	6.34	81
	19980607	15.70	5.21	56
	19990906	11.83	5.48	74
	20000714	13.98	5.91	88
	20020509	13.73	5.23	96
	20060901	10.29	4.58	102
	20070531	15.38	5.16	128
	20090909	7.12	4.14	29
	20100624	12.00	4.80	30

Chapter III:
Post-Soviet land-use change effects on large mammals' habitat in European Russia

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Abstract

Land-use change can strongly affect wildlife populations, typically via habitat loss and degradation where land use expands, but also via increasing potentially available habitat where land use ceases. Large mammals are particularly sensitive to land-use change, because they require large tracts of habitat and often depend on habitat outside protected areas unless protected areas are very large. Our research question was thus how land-use change around protected areas affects large mammals' habitat. Russia experienced drastic land-use change after the breakdown of the Soviet Union and – fortunately – wildlife data has been collected continuously throughout this time inside protected areas. We used long-term winter track count data for wild boar (*Sus scrofa*), moose (*Alces alces*), and wolf (*Canis lupus*) to assess habitat change inside and outside of Oksky State Nature Reserve from 1987 to 2007 using a time-calibrated species distribution model. Our results showed a constantly high share (at least 89%) of suitable habitat within the protected area's core zone for each species, yet also substantial habitat increases of up to 23% within the protected buffer zone, and similarly, up to 27% outside the protected area. Of the variables we evaluated, post-Soviet land-use change, particularly farmland abandonment, was the main driver of this expansion of potential habitat for the three species we assessed. Our study highlights that strictly protected areas have been playing an important role in preserving wildlife in European Russia since 1991, but also that their surroundings provide much suitable habitat for large mammals. Post-Soviet land-use change in the surroundings of protected areas may provide opportunities to increase and connect wildlife populations.

1 Introduction

Globally, biodiversity is declining and land-use change is a major reason for this (Sala et al. 2000; Foley et al. 2005). Agricultural expansion is particularly worrisome because it results in habitat loss, degradation, and fragmentation (Fischer and Lindenmayer 2007). This in turn can result in increased poaching, when new roads provide access into previously remote areas (Laurance et al. 2006; Coffin 2007), in changing water availability (Power 2010), and in invasive species spread (Brook et al. 2008). However, while agricultural expansion continues in many tropical regions (Phalan et al. 2013), agricultural abandonment has become a major land-use change trajectory, in tropical (Grau and Aide 2008; Aide et al. 2013) and temperate (Navarro and Pereira 2012; Schierhorn et al. 2013) regions. The biodiversity impacts of abandonment, however, are diverse and not well understood (Plieninger et al. 2014; Queiroz et al. 2014; Uchida and Ushimaru 2014).

Large mammals (i.e., body mass > 20 kg; Vynne et al. 2011) are particularly challenging to maintain in human-dominated landscapes (Dirzo et al. 2014). These species are typically wide-ranging and require large and well-connected habitat networks, and are thus especially prone to land-use change. Furthermore, large mammals often conflict with people, livestock, and cropping (Hoare 1999; Behdarvand et al. 2014), and are frequently poached for meat or trophies (Hilborn et al. 2006; Stokstad 2014). Declining populations of large mammals are worrisome because of their importance for ecosystems as their disappearance can result in cascading impacts via altering food webs and triggering ecosystem shifts (Estes et al. 2011; Ripple et al. 2014).

Protected areas are a key conservation tool to safeguard species' populations and their habitats against the direct impacts of land use, and ideally against its indirect effects as well. Yet, many protected areas are too small to harbor viable populations of large mammals (Newmark 1996) and these species depend on habitat surrounding protected areas. Prime examples include grizzly bears in the Greater Yellowstone Ecosystem (Carroll et al. 2004), giant armadillos and maned wolves in the Brazilian Cerrado (Vynne et al. 2011), Amur tiger in the Russian Far East (Carroll and Miquelle 2006), and Asian and African elephants (Galanti et al. 2006; Fernando et al. 2008). The surroundings of protected areas thus fulfill an important role for biodiversity conservation since they are part of the so-called 'zone of interaction' (DeFries et al. 2010), which represents the landscape comprising the protected area and its surroundings, which is linked to the protected area via multiple ecological processes and often strong interactions between humans and nature. At the same time, protected areas' surroundings are often intensively used which can make them populations sinks (Woodroffe and Ginsberg 1998). Therefore, it is important to evaluate how land-use change in the surroundings of protected areas affects wildlife habitat.

Evaluating the effects of land-use change on wildlife often hinges on the availability of habitat use data from before and after land-use change occurred. Long time series of species' presence records are particularly valuable in this context (Boulinier et al. 1998; Sauer et al. 2014; Bragina et al. 2015a). If longitudinal wildlife data are available, however, the challenge is how to analyze them given that data have been collected over many decades and while landscapes have changed. Time-calibrated niche models (Nogues-Bravo 2009; Kuemmerle et al. 2012) offer an approach to maximize the information gain from long-term species occurrence data, since all available data can be used in one model, which can then be used to predict habitat availability in places and times for which no observations exist (Reside et al. 2010; VanDerWal et al. 2013).

Information on habitat availability is important for large mammals' conservation, and in the case of large carnivores, additional information on biotic interaction is required, for example, the occurrence of prey species (Hebblewhite et al. 2014). Identifying suitable prey habitat is thus essential for maintaining and restoring carnivore populations and that may also help to minimize human-wildlife conflicts. So far, only a few studies addressed biotic interaction in species distribution models, such as including food resources (Bateman et al. 2012; Kuemmerle et al. 2012) or prey habitat as predictor for carnivore habitat models (Giannini et al. 2013; Hebblewhite et al. 2014). Generally, including biotic factors improves the predictive power of species distribution models (Wisz et al. 2013), yet applications that incorporate prey habitat distributions for assessing the habitat of predator species remain scarce.

Russia provides unique opportunities to understand the effects of land-use change on wildlife habitats within and outside of protected areas. The collapse of the Soviet Union in 1991 triggered drastic changes in socio-economic and institutional conditions, which in turn resulted in widespread land-use change including agricultural abandonment (Prishchepov et al. 2012a) and changes in forest harvesting (Baumann et al. 2012). Agricultural abandonment was especially widespread throughout European Russia and led to the expansion of transitional grassland and early successional forests. These changes in land cover have potentially substantial effects on wildlife by providing new habitats and connecting existing ones, at least in part contributing to the recent rebounding of large mammal populations in European Russia (Bragina et al. 2015a). However, the post-Soviet upheaval also caused considerable economic hardships (Klugman and Braithwaite 1998), lessened support for nature conservation (Wells and Williams 1998), and resulted in drastic population declines of many large mammal species in Russia, except for wolves during the 1990s (Bragina et al. 2015a).

Fortunately, Russia's protected areas were the focus of truly exceptional long-term biodiversity monitoring. Most of the 103 strictly protected state nature reserves ('zapovedniks', IUCN category Ia; IUCN and UNEP-WCMC 2014) have permanent scientific staff who collected a broad range of biodiversity and ecosystem variables for decades, using standard survey protocols, and published these in the so-called Chronicles of Nature (Летописи природы) every year (Spetich et al. 2009). An important element of the protected areas' biodiversity monitoring are winter track counts (WTC, Зимний маршрутниый учёт) that provide species' occurrence maps and estimate large mammal population sizes (Carroll and Miquelle 2006; Stephens et al. 2006; Bragina et al. 2015a). In some protected areas, WTC have been collected since the 1960s (Lomanov 2007), thus providing a baseline from Soviet times and covering the entire transition period of rapid socio-economic and land-use change after 1991.

Understanding how land-use change affects wildlife habitat, and how these land-use changes may affect the zone of interaction surrounding protected areas is important for identifying effective strategies to protect large mammals, which can rarely survive inside protected areas alone. European Russia provides unique opportunities to learn more about these issues in general, because land-use change there has been drastic in response to the socio-economic and institutional shocks of the breakdown of the Soviet Union, and because longitudinal wildlife data have been collected in a standardized manner for decades, including the period of rapid land-use change. Our overarching goal thus was to evaluate how post-Soviet land-use change affected the distribution of potential habitat for large-mammals both inside protected areas and in their surroundings. To explore this question, we analyzed a long-term dataset of annual winter track counts for three large mammals, wild boar (*Sus scrofa*), moose (*Alces alces*), and wolf (*Canis lupus*), from Oksky State Nature Reserve, in the temperate zone of European Russia. The three species represent the largest and most wide-ranging mammals in our study region and have different habitat requirements since they are omnivore, herbivore, and carnivore species, respectively. We related the wildlife data to land-use change information derived from Landsat satellite images in order to map the availability of potential habitat inside and outside the protected area using a time-calibrated species distribution model. We furthermore assessed the impact of including information on prey habitats to model potential habitat of a large carnivore species. Our a priori hypothesis was that land-use change has led to an increasing availability of potential habitat for our target species – both inside and outside the protected area. We also assumed the inclusion of prey variables will improve the prediction of large-carnivore habitat. Specifically, our objectives were:

1) To model habitat selection of wild boar, moose, and wolf using a time-calibrated species distribution model, and to predict habitat distribution for different time periods,

2) To assess changes in habitat availability of the three targeted large mammal species within Oksky State Nature Reserve and its immediate surroundings from 1987 to 2007 due to post-Soviet land-use change, and

3) To explore the relative importance of including prey habitat distributions for analyzing predator habitats.

2 Material and methods

2.1 Study area

Our study area is located in temperate European Russia in Ryazan Oblast and includes Oksky State Nature Reserve and its surroundings (Figure III-1 and Figure III-S1 in the Supporting Information). The study area covers about 800,000 ha and falls within the sarmatic mixed forest ecoregion (Olson et al. 2001) with mainly coniferous and mixed forests, dominated by spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and pedunculate oak (*Quercus robur*) on glacial, sandy soils. Its southern and eastern boundary is the floodplain area of the Oka River with extensive riverine grasslands. The study area is characterized by flat terrain ranging from 76 m to 172 m. The climate is moderate, with highest mean temperature in July (20 °C) and lowest in February (-12 °C), and an annual precipitation of about 534 mm (Priklonsky and Tichomirov 1989).

About 10% of the study area is managed by the Oksky State Nature Reserve. This federal strictly protected area was established in 1935, originally to protect the Russian desman (*Desmana moschata*) and the wetland around the Pra River, a tributary of the Oka River. In 1978, Oksky State Nature Reserve became a biosphere reserve and in 1989, a transition zone of 33,000 ha and a buffer zone of 22,000 ha were added to the 23,000 ha core zone (Figure III-1). The core zone is strictly protected, all land use is prohibited, and access is limited to scientists and protected area staff only. In the transition zone, non-timber forest products (e.g., mushrooms and berries) can be collected. In the buffer zone, sustainable land management is the overarching goal (Ivanchev 2009, 2011, personal communication; MAB 2010). Three large mammals are emblematic of the protected area today: wild boar, moose, and wolf.

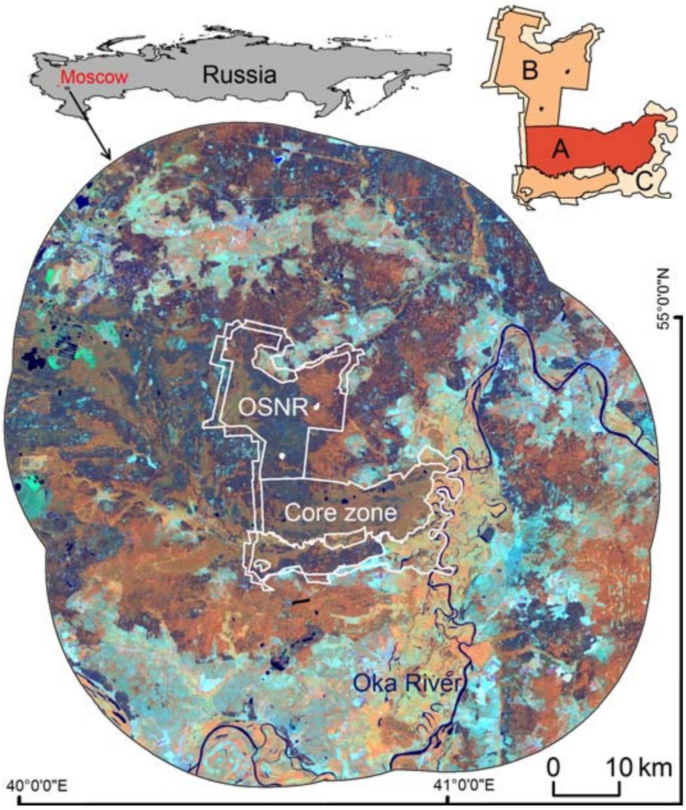

Figure III-1: Study area with Oksky State Nature Reserve in Russia and related biosphere reserve zoning (A = core zone, B = transition zones, and C = buffer zone) and the protected area's surroundings (Landsat TM 5 image in 4-5-3 false colors from 31st May 2007).

After the collapse of the Soviet Union in 1991 widespread land-use changes occurred across Russia (Achard et al. 2006; Alcantara et al. 2013), mainly due to a combination of declining rural populations and the diminishing profitability of agriculture due to the reduction of state-support, price liberalization, and disappearing markets within the former Soviet sphere of influence (Prishchepov et al. 2013). For example, the rural population in Ryazan Oblast declined from 1987 to 2007 by 24% (ROSSTAT 2013) and in our study area, about 40% of the farmland in use in 1988 was abandoned by 2010 (Sieber et al. 2013). Most importantly, vast areas of former pastures were abandoned when the region's livestock sector collapsed (cattle, pig, and sheep numbers decreased by more than 75%

from 1987 to 2007 in Ryazan Oblast; ROSSTAT 2008). As of 2010, many abandoned areas were encroached by shrubs or young forests. In terms of forest management, logging rates decreased by 50% in 2000 compared to the mid-1980s (Sieber et al. 2013). Thus, human pressure in terms of land use appears to having decreased in the post-Soviet period in our study area.

2.2 Species occurrence data

Long-term winter track counts (WTC) of all three large mammals were collected by co-author Nikolai V. Uvarov along transects within the core zone of Oksky State Nature Reserve. Data for wild boar were collected consistently from the winter of 1978/9 to 2007/8, for moose from 1992/3 to 2008/9, and for wolf from 1994/5 to 2008/9. Each year from October until March, transect locations and species tracks crossing these transects were noted based on fresh snow. We scanned the WTC maps, georeferenced them, and digitized the occurrence points for each species and year (Figure III-S2 in the Supporting Information). To avoid pseudo-replication, we overlaid the occurrence points for each species and year with a 100-m grid and randomly selected one point in cells with multiple points (Elith et al. 2011).

2.3 Environmental and human-impact variables

To analyze habitat selection and to map suitable habitat, we compiled a set of environmental and human-impact variables that were assumed to affect wildlife habitat suitability in our study area. Variable selection is a crucial step for modelling wildlife habitats (Velez-Liendo et al. 2013). Candidate variables were identified based on the literature and expert knowledge (Table III-1), and we used variables on land cover and land use, topography, human disturbance, and biotic interactions in our analyses. In terms of land cover and land use, we included information on, for example, different forest types, neighborhood information on the percentage of farmland and unmanaged grassland, and the Euclidean distances to core and edge forests. All of these variables were available for the years 1987, 1994, 1997, 2002, and 2007. In addition, we included the time-invariant variables for topography (e.g., elevation and slope) and human disturbance (e.g., Euclidean distance to roads) as control factors (Table III-1 and Table III-S1 in the Supporting Information).

Table III-1: Variable selection for modelling suitable wildlife habitats in the study area. The terrain and human disturbance variables are time-invariant, whereas all other variables were available for the years 1987, 1994, 1997, 2002, and 2007. The detection of farmland abandonment, i.e., the conversion from farmland to unmanaged grassland, was based on two Landsat TM/ETM+ satellite image classifications and resulted in separate farmland abandonment maps for the years 1994/97 and 2002/07.

Variable	*Comments*	*Source*	*Data type and range*
Land cover/land use			
Land cover	9 classes: background, farmland, unmanaged grasslands & riparian trees, forest, forest disturbances, coniferous forest, oak (*Quercus*) and linden (*Tilia*) forest, deciduous forest, and mixed forest	Landsat TM/ETM+ images (Sieber et al. 2013); Forest-type map of Oksky State Nature Reserve	Categorical; Classes 1-9
Fraction of farmland	Percent of farmland in a 2-km neighborhood	Landsat TM/ETM+ images	Continuous; 0-100%
Fraction of grassland	Percent of unmanaged grassland (and riparian trees) in a 2-km neighborhood	Landsat TM/ETM+ images	Continuous; 0-100%
Distance to core forest	Euclidean Distance in m; calculated with Morphological Spatial Pattern Analysis (MSPA) using GUIDOS software (Vogt et al. 2007), edge width: 30 m	Landsat TM/ETM+ images	Continuous; 0-3,700 m
Distance to forest edge	Euclidean Distance in m; calculated with MSPA (Vogt et al. 2007), edge width: 30 m	Landsat TM/ETM+ images	Continuous; 0-3,000 m
Terrain			
Elevation	In m	Shuttle Radar Topography Mission (SRTM) of the United States Geological Survey (USGS)	Continuous; 76-172 m
Slope	In degrees, calculated from the elevation variable	SRTM USGS	Continuous; 0-11.1 °
Human disturbance			
Distance to roads	Euclidean distance in m	Soviet 1:100,000 topographic maps	Continuous; 0-8,000 m
Biotic interactions			
Wild boar and moose as prey for wolf	Predictions of potential habitat for wild boar and moose (Maxent outcomes)	Winter track counts of Nikolai V. Uvarov from Oksky State Nature Reserve, Russia	Continuous; 0-1

To model the habitat of wild boar and moose, we used all of these variables. To model the habitat for wolf, we used these variables plus potential wild boar and moose habitat (i.e., the respective relative habitat suitability index outcome scaled between 0 and 1, see section 2.4 and Table III-1), since wolves prey on both ungulates. We additionally parameterized a second wolf model without any prey habitat variables and a third wolf model with only wild boar habitat as a prey variable to explore the relative importance of including the prey variables (Table III-S2 in the Supporting Information). We selected wild boar habitat as the only prey-related variable in the third model because the wild boar variable performed slightly better than an alternative model including only the moose habitat variable (Table III-S2).

2.4 Time-calibrated habitat modeling

Species distribution models (SDM) are powerful tools to explore spatial patterns of wildlife habitat (Elith et al. 2006; Hegel et al. 2010). SDM describe a species' potential distribution by estimating the relationship between species occurrences and the environmental characteristics at these sites (Elith and Leathwick 2009). Typically, SDM are either based on data for a single snapshot in time (e.g., a recent land-cover classification), or on mean values (e.g., average temperature). Snapshots in time do not capture habitat changes, and mean values can easily obfuscate crucial environmental conditions that occurred during the time that the occurrence record was collected. One approach to account for changing environmental conditions would be to derive unique habitat models for each time step. However, this is rarely feasible because this requires large numbers of occurrence records and would still bear the risk of underestimating true habitat suitability if species do not occupy all potentially suitable habitats in a given time step (Nogues-Bravo 2009; Franklin 2010).

The alternative is to apply a time-calibrated species distribution model (Nogues-Bravo 2009; Kuemmerle et al. 2011b). A time-calibrated SDM is a single model parameterized for the entire time period of interest, trained with data from all time periods represented in the occurrence points (i.e., multiple years in our case). To parameterize the time-calibrated model, occurrence records are matched with the environmental conditions from the time when the occurrence point was recorded. The resulting single SDM is thus independent from a particular time period and can be projected to each time period for which a set of predictors is available. Thus, a time-calibrated SDM allows to predict changes in habitat availability over time as well as to assess habitat distribution for time periods in which occurrence data may be unavailable. Moreover, model outcomes for each time step are comparable, because they rely on the same time-calibrated model. We calibrated our SDM with the occurrence data available for the winter periods of 1994/5, 1997/8, 2002/3, and 2007/8 for each of the three species, respectively.

We used maximum entropy modeling (Maxent, Phillips et al. 2006), a machine-learning approach, widely applied for species distribution modeling (Elith et al. 2011). As an SDM algorithm, Maxent frequently outperforms other presence-only modeling techniques (Elith et al. 2006; Hernandez et al. 2006; van Gils et al. 2014). We used the Maxent version 3.3.3k available at www.cs.princeton.edu/~schapire/maxent/. We tested all predictor variables for collinearity by calculating pairwise Pearson's correlation coefficients based on 5,000 random points to facilitate interpreting the variable importance. We found strong correlation ($r > 0.8$) between the two prey habitat variables ($r = 0.93$). Even though model performance in Maxent is generally not sensitive to collinearity (Elith et al. 2011), collinearity can hinder model interpretation (Dormann et al. 2012). We therefore evaluated the relative variable importance based on single-variable models and based on comparing wolf models with none, only one, or both prey habitat variables, and selected the model with the best performance (in our case the wolf model using both prey variables) for predicting wolf habitat. Furthermore, we also did not allow for extrapolation into environmental conditions not covered by our input data using the 'clamping' function in Maxent as a precautionary measure (Phillips et al. 2006).

We ran our time-calibrated models for each of the three wildlife species using a sample of the WTC occurrence points. We used the same number of points per time step to avoid bias due to potentially changing species abundance over time. Sample size was determined by the smallest amount of occurrence points for a given year (i.e., 80 random points per year for wild boar, and 250 points for moose and wolf, respectively). Maxent then contrasts the environmental characteristics at the occurrence locations with those at a random set of background points. As the WTC were mainly collected inside Oksky State Nature Reserve, our occurrence dataset was based on an uneven sampling effort. To account for this, we used a bias file for background point selection, i.e., a mask restricting the random sampling of background points to those areas where occurrence points were sampled. To do so we used a maximum convex polygon around the sampling transects and occurrence points plus a 100-m buffer (Phillips et al. 2009; Elith et al. 2011). We randomly selected 5,000 background points (Phillips and Dudik 2008; Elith et al. 2011; Renner and Warton 2013), and assigned 1,250 points to the environmental conditions of each of the four time steps, respectively (Table III-S1).

We evaluated our models based on 10-fold cross-validation in two ways. First, we used the area under the curve (AUC) value of the receiver operating characteristics (ROC) curve to evaluate model performance (Phillips et al. 2006). Second, we evaluated the relative importance of variables to identify the variables with highest impact using a) jackknife estimates of the AUC and relative gain changes by either using a single-variable model or dropping single variables compared to the full model, and b) response curves of single-variable models (Kuemmerle et al. 2010; Elith et al. 2011). Based on the best-performing (highest AUC) models for each species, we made predictions for Oksky State Nature Reserve and a 30-km buffer around it, and for each time step for which environmental variables were available (1987, 1994, 1997, 2002, and 2007). Suitable habitat was defined as areas with suitability index values above the minimum predicted value (i.e., minimum training presence logistic threshold; Phillips et al. 2006; Anderson and Raza 2010), meaning that all values predicted at actual occurrence points were assumed to represent suitable habitat. Finally, we evaluated whether changes in the predicted habitat over time were significant at the 0.05 level by applying the SigDiff function (available in the R package SDMTools; Januchowski et al. 2010; Bateman et al. 2012), which quantifies the significance of pairwise differences relative to the mean and variance of all differences between two habitat maps, and provides a map highlighting areas where significant differences occur.

3 Results

3.1 Habitat selection

We parameterized models that were generally robust and resulted in reasonable maps of habitat suitability for all three large mammals we studied (Figure III-S3 in the Supporting Information). The best-performing models had an AUC of 0.77 for wild boar, 0.73 for moose, and 0.68 for all three wolf models, and standard errors of 0.01 for all species. Of the eight variables included to the SDM for ungulates, those with the highest relative importance were elevation, land cover, and distance to core forest for wild boar, as well as elevation, distance to roads, and land cover for moose (Table III-S2). The predicted suitable winter habitat for wild boar in our study was at elevations around 100 m, more than 3 km away from roads, within deciduous forest including oak and linden (*Tilia*) and coniferous forest, with only little farmland in the neighborhood, but up to 25% grassland, and preferable close to the forest edge. Preferred habitat for moose was similar to that of wild boar, except for grasslands being of greater importance, both in the land-cover variable and in the neighborhood variable.

Of the ten variables available to model potential wolf habitat, the prey-related variables (i.e., wild boar habitat and moose habitat) as well as elevation, fraction of grassland, and distance to forest edge were the most important based on the single-variable models (Table III-S2). To further explore the relative variable importance, we compared the wolf model with both prey variables to a wolf model without prey variables, and a model including only wild boar habitat. We found that land cover, elevation, and the fraction of farmland provided the most unique information based on AUC decrease when one of these variables was dropped (Table III-S2). In general, the predicted habitat characteristics for wolf were similar to those of the prey species, besides a smaller distance to roads (2-5 km).

3.2 Habitat availability

We defined suitable habitat as the area with habitat suitability values greater than the minimum predicted value, which was 0.10 for wild boar, 0.03 for moose, and 0.12 for wolf. Our results showed that the area of suitable habitat for all three wildlife species changed substantially over time. In Soviet times, wild boar habitat covered ca. 110,980 ha, a total share of 15% of the study region (Figure III-2, Table III-S3 in the Supporting Information). Over the next 20 years, wild boar habitat increased to a total share of 17% in 2007 (ca. 124,010 ha). Habitat gain was higher in the first period until 1997 (9% increase in habitat area from 1987 to 1997) than until 2007 (3%). The increase in suitable habitat was significant at the 0.05 level (Figure III-S4 in the Supporting Information) and occurred mainly in areas adjacent to forest that were already predicted as suitable in the preceding time periods and in areas outside of Oksky State Nature Reserve where regrowing forests occurred on abandoned farmland. The share of suitable habitat within the protected area was generally higher than in the unprotected surroundings. Wild boar habitat always occupied most of the core zone of Oksky State Nature Reserve (>89%; Figure III-3). In contrast, only 21% of Oksky's transition zones were suitable habitat in 1987 (ca. 7,100 ha, slightly increasing by 180 ha until 2007). In the buffer zone, the share of wild boar habitat was equally low in 1987, however, suitable habitat increased by 10% (ca. 450 ha) until 2007. The surroundings of Oksky State Nature Reserve had the smallest share of wild boar habitat (79,350 ha or 12% in 1987), even though the increase was largest (12,320 ha, or 16% growth by 2007).

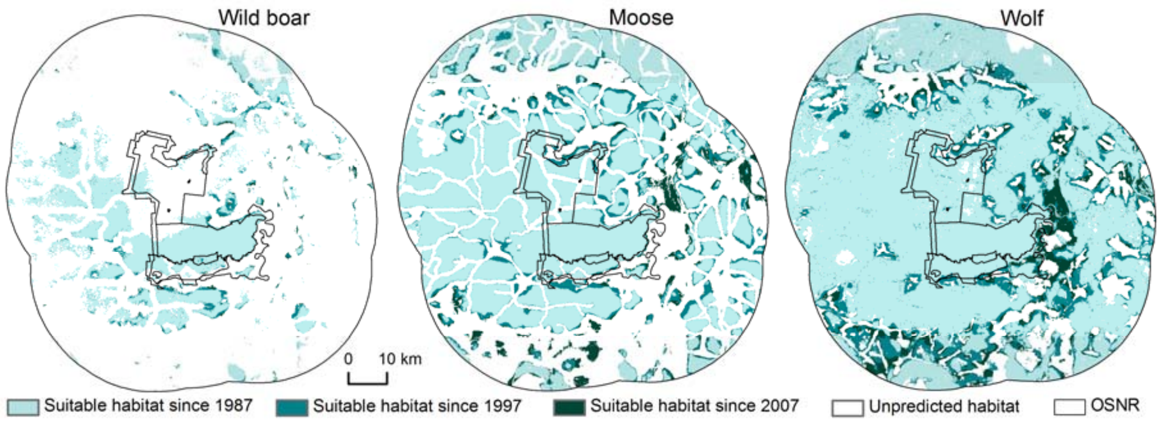

Figure III-2: Changes in predicted suitable habitat for wild boar, moose, and wolf within and outside Oksky State Nature Reserve (OSNR) from 1987 to 2007 (based on the minimum training presence logistic threshold).

Moose habitat increased to an even greater extent in our case. In 1987, 42% of our study area was predicted suitable (314,990 ha; Figure III-2, Table III-S3). Until 2007, moose habitat increased by 23%, which equals a gain of ca. 72,210 ha, leading to a share of 52% suitable habitat in our study region (ca. 387,200 ha). Most of this increase occurred in the 1990s, right after the breakdown of the Soviet Union. Moose habitat expanded especially into areas that were agriculturally used (cropland or pastures) during Soviet times, but were abandoned after 1991. Furthermore, habitat gain was significant at the 0.05 level (Figure III-S4) and mainly occurred conterminous to areas predicted as suitable habitat in earlier time slots investigated. Similar to wild boar, new habitat occurred mainly outside of Oksky State Nature Reserve, whereas there was always a higher share of suitable habitat within the protected area. The core area of Oksky State Nature Reserve was effectively suitable moose habitat throughout the entire time we investigated (>98%; Figure III-3). Within the transition zones, 70% of the area was predicted suitable for moose in 1987 (ca. 23,290 ha), increasing to 72% in 2007 (ca. 23,830 ha). The buffer zone had a share of 45% of moose habitat in 1987 (ca. 9,820 ha) that increased substantially to 55% in 2007 (ca. 12,120 ha), resulting in a gain of 23% of the 1987's area. Nevertheless, this growth of suitable potential habitat for moose was even exceeded in the surroundings of Oksky State Nature Reserve, where 259,580 ha in 1987 increased to 328,910 ha in 2007, equaling an increase of 27% of the 1987's area.

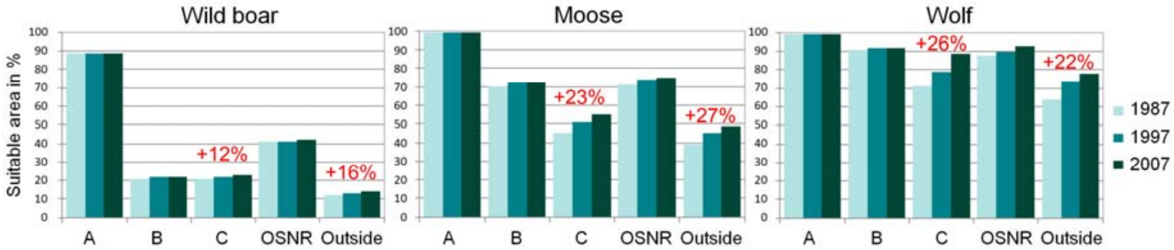

Figure III-3: Percentage of area with predicted suitable habitat for wild boar, moose, and wolf within the entire Oksky State Nature Reserve (OSNR), the three zones of the biosphere reserve (A = core zone, B = transition zones, and C = buffer zone), and the 30-km surrounding of the protected area (outside) for three time steps. The percentages of relative area changes from 1987 to 2007 are highlighted in Red for the protected area's buffer zone and the surroundings.

Suitable wolf habitat covered the largest portion of our study area of any of the three wildlife species we investigated, for the first wolf model a total of 494,370 ha in Soviet times, or 66% of the study area (Figure III-2, Table III-S3). Until 2007, wolf habitat increased by 20%, ca. 98,380 ha, for a total of 592,740 ha (79%). Again, most of the increase occurred until 1997, when wolf habitat gained twice as much area as in the second period from 1997 to 2007. Habitat expanded significantly (0.05 level; Figure III-S4) and mainly onto abandoned fields close to settlements and in the floodplain areas of Oka River and its tributaries. The wolf model omitting the prey habitat variables showed different results, with less predicted suitable habitat across time (26% unpredicted habitat versus 17% for the first wolf model; Figure III-4) and an always smaller share. In 1987, the share of predicted suitable wolf habitat was slightly smaller (65%; 488,090 ha) than for the wolf model with both prey variables, but substantially decreased from 1997 (71%) to 2007 (58%; Figure III-4; Table III-S3). Compared to the ungulates, wolf habitat also had the highest shares of potential habitat inside and outside of Oksky State Nature Reserve. Wolf habitat almost completely covered the core zone with >99% of the area ranked as suitable habitat across all years, and occurred in >91% of the transition zones' area (Figure III-3). Habitat gain in our study period was largest for the buffer zone. Here, a share of 71% in 1987 (ca. 15,570 ha) increased to 89% in 2007 (ca. 19,600 ha), resulting in a gain of 26% of the 1987's area. Within the surroundings of the protected area, wolf habitat covered 64% of the area in 1987 (ca. 426,250 ha), expanding to 78% in 2007 (ca. 520,320 ha), which corresponded to an increase of 22% of the 1987's area.

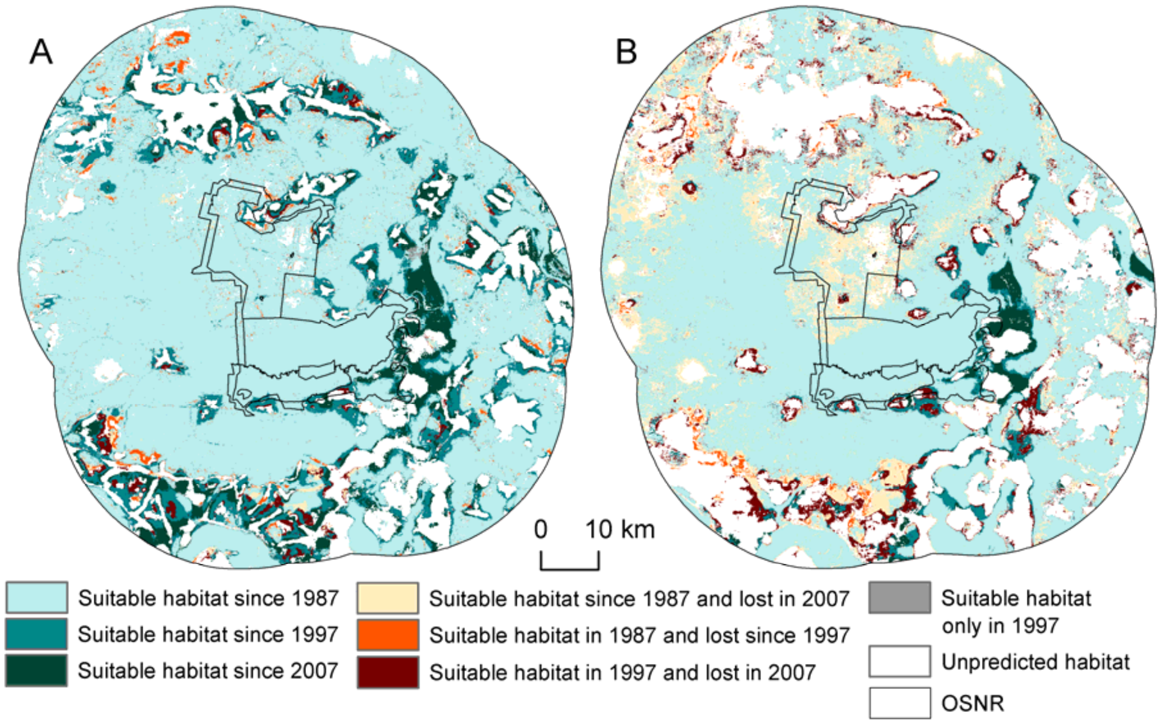

Figure III-4: Predicted suitable wolf habitat within and outside Oksky State Nature Reserve (OSNR) for the model including prey-related habitat variables (A) and the model without prey habitat variables (B) for three time steps.

4 Discussion

4.1 Habitat selection and availability

The collapse of the Soviet Union in 1991 triggered widespread land-use change and we found an increase in potentially suitable habitat of large mammals in response. The factors we identified as influential for determining the habitat selection of the three large mammals we investigated were well in line with prior studies. For example, the presence of deciduous forests with oak mast and coniferous forest stands were important in determining wild boar habitat in Poland (Fonseca 2008), Sweden (Thurfjell et al. 2009), and Europe in general (Melis et al. 2006), and the availability of deciduous forests and grassland as well as large distances to roads affected moose habitat selection in Sweden (Neumann et al. 2012) and Russia (Heptner et al. 1988; Baskin and Danell 2003). Interestingly, and in contrast to other studies, we found that elevation was important in determining ungulates' habitat selection, which may be due to the digital elevation model of the Shuttle Radar Topography Mission (SRTM) that also captures land cover since the radar waves may not penetrate the vegetation canopy, and the data thus do not represent the ground surface (Farr et al. 2007). In terms of wolf habitat, our study confirmed the generalist nature of wolves, and the importance of human disturbance as a driver of habitat selection as in Poland (Jedrzejewski et al. 2004) and Canada (Lesmerises et al. 2012). Wolves are a special case in Russia for the post-Soviet period (Bragina et al. 2015a) because they were the only large mammal with increasing populations during the 1990s, as a result of decreasing wolf persecution then. In our case, wolf habitat increased since 1991, possibly at least in part due to more widespread ungulate habitat, given that wild ungulates are the main prey of wolf in Eastern Europe (Okarma 1995), and the collapse of livestock farms substantially reduced feeding opportunities on carcasses after 1991 (Gubar 2000), yet wolf populations still increased (Bragina et al. 2015a).

From 1987 to 2007, the area of suitable habitat for the three wildlife species we investigated increased up to 23%. Several reasons explain this increase. First, post-Soviet land-use change, particularly farmland abandonment, was widespread in Eastern Europe (Alcantara et al. 2013; Estel et al. 2015). In our study area, mainly marginal farmland in the vicinity of forests was abandoned, and most abandonment happened in the early 1990s (Prishchepov et al. 2012a; Sieber et al. 2013), whereas the succession of shrubland and forests on farmland far away of the forest edge happened delayed. Yet, as in other regions characterized by large-scale farmland abandonment, regrowing natural vegetation likely provided forage and shelter important to wildlife in our case as well (Bowen et al. 2007; Plieninger et al. 2014), and may have increased habitat connectivity among existing habitat patches (Sitzia et al. 2010; Hernandez et al. 2015). As a result, post-Soviet land-use change and the recovery of large mammal populations in the 2000s (Bragina et al. 2015a) may be interpreted as signs of large-scale rewilding, similar to trends in some parts of Western Europe (Navarro and Pereira 2012; Ceaușu et al. 2015).

A second reason contributing to the increasing availability of potential habitat for our species was the expansion of protected areas in our study area. The current core zone of Oksky State Nature Reserve represented the entire protected area from 1935 to 1988 and was strictly protected throughout, resulting in a high share of suitable wildlife habitat there. In contrast, forestry and agriculture in the transition zone were restricted only after 1989, when the biosphere reserve regulations were implemented (MAB 2010), and these restrictions contributed to the increasing availability of wildlife habitat in this zones (Figure III-3). Land use in the buffer zone is not restricted, however, yet we still found declining land-use pressure and farmland abandonment in this area. Increasing habitat quality in this zone was therefore mostly due to the socio-economic and institutional changes in the aftermath of the breakdown of the Soviet Union. Similarly, the landscape surrounding the biosphere reserve changed much in post-Soviet times, creating new suitable habitat over time, and potentially connecting suitable habitat within the protected area and in its surroundings. Post-Soviet land-use change and the expansion of buffer zones thus improved large mammal habitat quality and availability in the protected area's zone of interaction (Hansen and DeFries 2007), a trend opposite to most other world regions where protected areas are becoming increasingly isolated (Newmark 1996; DeFries et al. 2005). How increasing habitat availability and connectivity in post-Soviet Russia affected mammals' populations would be worthwhile to explore in future research.

Including biotic information into models evaluating the habitat selection of large mammal species has been shown to improve model performance and outcomes (Hebblewhite et al. 2014) and our study provides further evidence for this. We assessed the habitat suitability for wolf and compared models with and without prey habitat variables. Although both model types resulted in overall relatively similar wolf habitat maps, and similar conclusions about wolf habitat selection (Figure III-2 and Figure III-4), including prey habitat improved model performance and highlighted more potentially suitable habitat patches than models without these variables. This suggests potentially suitable habitat for large carnivores may be underestimated if prey habitat is not taken into account, and there is a benefit of including multiple prey species in cases where the habitat selection of these species differs such as in the case of wild boar (generalist) and moose (forest specialist). However, as the prey habitat variables are the result of an SDM application, we caution that uncertainty in this modelling exercise may propagate into the results of the wolf habitat model. In our case, including the prey variables improved model performance, similar to prior studies (Giannini et al. 2013; Hebblewhite et al. 2014).

4.2 Limitations

We evaluated potential wildlife habitats by applying time-calibrated species distribution models, yielding generally good model fits and plausible habitat maps. Still, several sources of uncertainty need mentioning. First, we analyzed winter track count data, and thus modeled winter habitat. However, we did not have fine-scale, spatially explicit data on winter severity or snow cover, which can be crucial for the survival of large ungulates and large carnivores (Nasimovich 1955; Baskin and Danell 2003). Some of our predictors may thus act as proxies for weather variability across the study region (e.g., elevation as a proxy for snow depth). Second, we mapped only winter habitat, the most critical time period for all species we investigated, and summer habitat may be more widespread. While this would not impair comparisons over time, focusing on winter habitat means that our estimates of potentially available habitat are conservative. Third, our species occurrence points were collected along transects and did not represent a fully random sample of points. Yet, the risk of potential bias induced by non-random transect placements seems small, because transects cover the entire core zone of Oksky State Nature Reserve, and we randomly sampled from all occurrence data using a minimum distance between points. Further, we addressed the issue of a potential sampling bias by limiting the random background point selection (Phillips et al. 2009). Although we cannot fully rule out remaining bias, our models did not suggest that we extrapolated in environmental space when projecting to the entire study region.

Fourth, our species occurrence data did not account for potentially varying hunting pressure. Human pressure, and especially hunting, is crucial in determining the habitat selection (Keuling et al. 2008; Thurfjell et al. 2009). Although we addressed this in our modeling approach, we could only use relatively indirect proxies for hunting and human pressure (e.g., distance to roads as a proxy for accessibility of a location to hunters). Wild boar and moose are important game species (Fonseca 2008), and all areas outside the Oksky State Nature Reserve are subject to hunting. More direct spatial measures of hunting, both legal hunting and poaching, would have been desirable, but do not exist to the best of our knowledge. Fifth, our species occurrences did not cover the full gradient of land-use intensity in our study area, as the most intensive land uses are not found inside the protected areas. Our model outcomes may thus underestimate wildlife habitat availability for species that are tolerant to land use, which may especially be the case for more generalist species (e.g., wild boar). At the same time, the availability of suitable habitat might be overestimated for wildlife species sensitive to land management. Sixth, as with any SDM, our model only predicts potentially suitable habitat, but cannot attest to whether or not habitat is actually used. This would be particularly relevant if hunting pressure was high, for example, due to high poaching during the 1990s (Bragina et al. 2015a), meaning that not all habitat that we identify may have been occupied during that period. Likewise, changing legal hunting pressure may also lead to some of the potential habitats not being occupied.

Seventh, our models achieved moderate AUC values (Franklin 2009), ranging between 0.7 and 0.8. Lower AUC values are to be expected for generalist species such as wild boar and wolf, because the contrast between occurrence and background points can be low if a species is using a wide range of habitat (Lobo et al. 2008). Finally, to discriminate suitable from unsuitable habitat, we decided to use the minimum predicted value (i.e., minimum training presence logistic threshold; Elith et al. 2006; Pearson 2007) as our threshold, because our occurrence data were of high spatial precision and because our species are all generalists. Thus, our focus here was on avoiding omission errors, and on identifying all habitat suitable for these species rather than to only identify best, or only high quality habitat. More conservative thresholds would result in a proportional decline of predicted increase of suitable habitat, yet would not affect our conclusions about relative habitat change inside and outside the protected area (Figure III-S3).

4.3 Conservation implications

In summary, we analyzed a long-term dataset on large mammal occurrence, spanning 20 years from 1987 to 2007, to assess the effects of widespread land-use change after the collapse of the Soviet Union on wildlife habitat and how these land-use changes affected the zone of interaction surrounding protected areas. While the land changes that happened in the wake of the collapse of the Soviet Union were unusual in magnitude, our time-calibrated species distribution models are broadly applicable and could be used for any protected area and for any land-use change as long as longitudinal wildlife data and land-change maps are available.

Finally, our study highlights that strictly protected areas provided suitable habitat for emblematic species throughout the post-Soviet transition period. Many wildlife populations were declining in the 1990s, likely due to overharvesting (i.e., poaching as a result of lower levels of control and a period of economic hardship; Bragina et al. 2015a) and rebounded after 2000 as socio-economic conditions became more stable (Hanson 2009) and poaching decreased. Given that protected areas in European Russia remained relatively effective after the breakdown of the Soviet Union (Sieber et al. 2013; Wendland et al. 2015), it appears that these areas played an important role as havens for large mammals during times of instability and raising pressure on wildlife from poaching (Bragina et al. 2015a), which might not be the case in other regions (Craigie et al. 2010). Given that globally many regions of conservation are unfortunately experiencing turbulent institutional and socio-economic times, our study thus highlights the potential gains of supporting conservation action even during such times. However, our study also shows that habitat effects occur lagged, as vegetation succession took time, and can only translate into a benefit for wildlife populations once more direct threats to species' survival (poaching in our case) are curbed.

Our results indicated that the pulse of farmland abandonment that occurred after 1991 initiated in a phase of rewilding, with decreasing human impact and expanding potential wildlife habitat. Across Europe, such rewilding trends are increasingly observed, with recovering large mammal populations (Chapron et al. 2014). Continued abandonment in some European regions is likely (Verburg et al. 2010) and other world regions may see declining agricultural areas in the future, too (Meyfroidt and Lambin 2011). Conversely, rising demand for agricultural commodities may lead to a reversal of recent abandonment trends, as already seen across some parts of the former Soviet Union (Kamp et al. 2011; Estel et al. 2015). This suggests we may be in a critical moment for implementing conservation action that can benefit large-bodied and wide-ranging species, and thus biodiversity in general. Future analyses highlighting which currently abandoned areas are most important in terms of providing connectivity in the habitat network of large mammals would be particularly important for conservation planning – in European Russia and elsewhere.

Acknowledgments

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Supporting Information

Additional information on the environmental characteristics in the study area and the species occurrence data

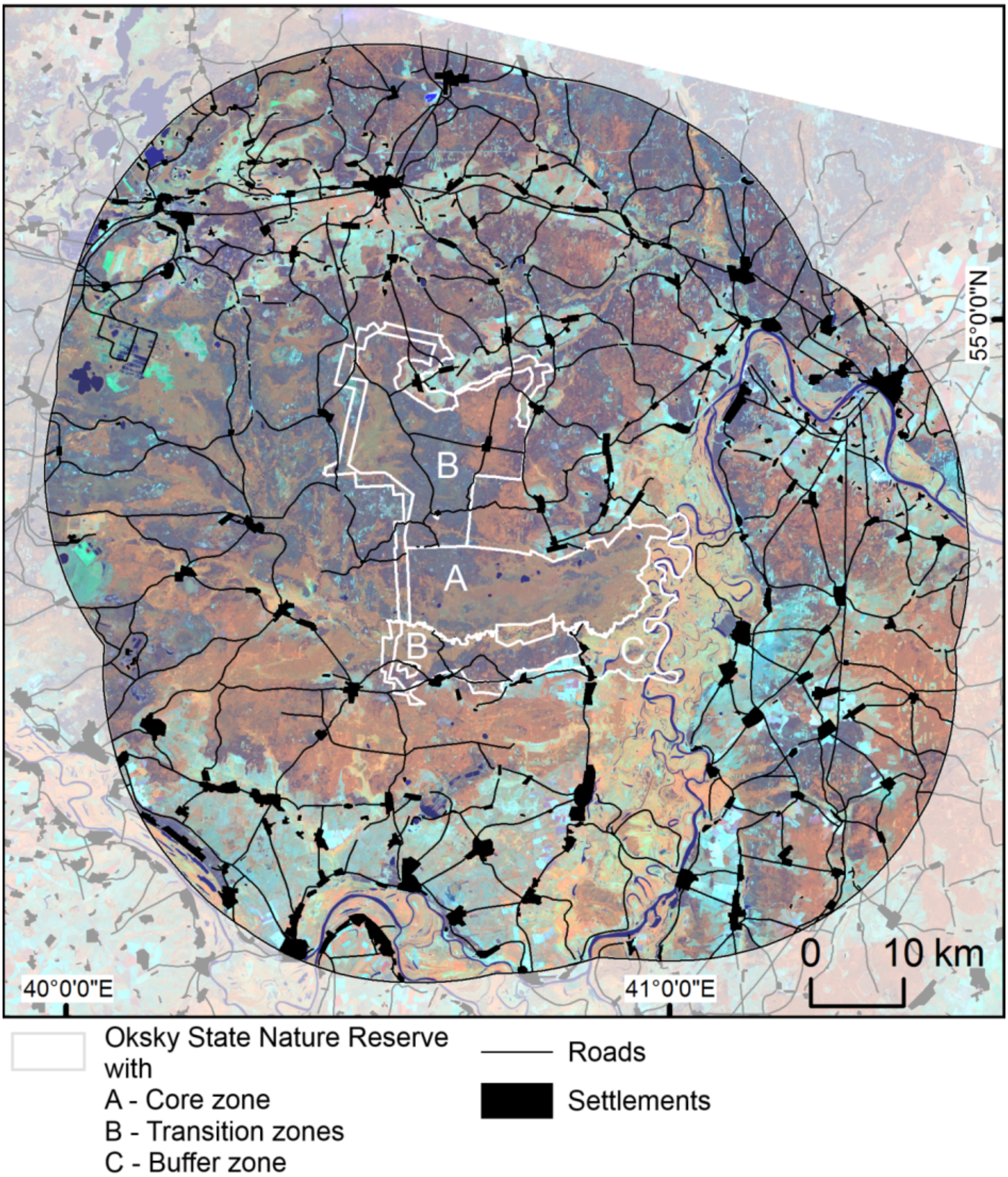


Figure III-S1: Study area with Oksky State Nature Reserve including related biosphere reserve zoning and the protected area's surroundings (30-km distance) with roads and settlements on a satellite image (Landsat TM 5 image) in 4-5-3 false colors from 31st May 2007.

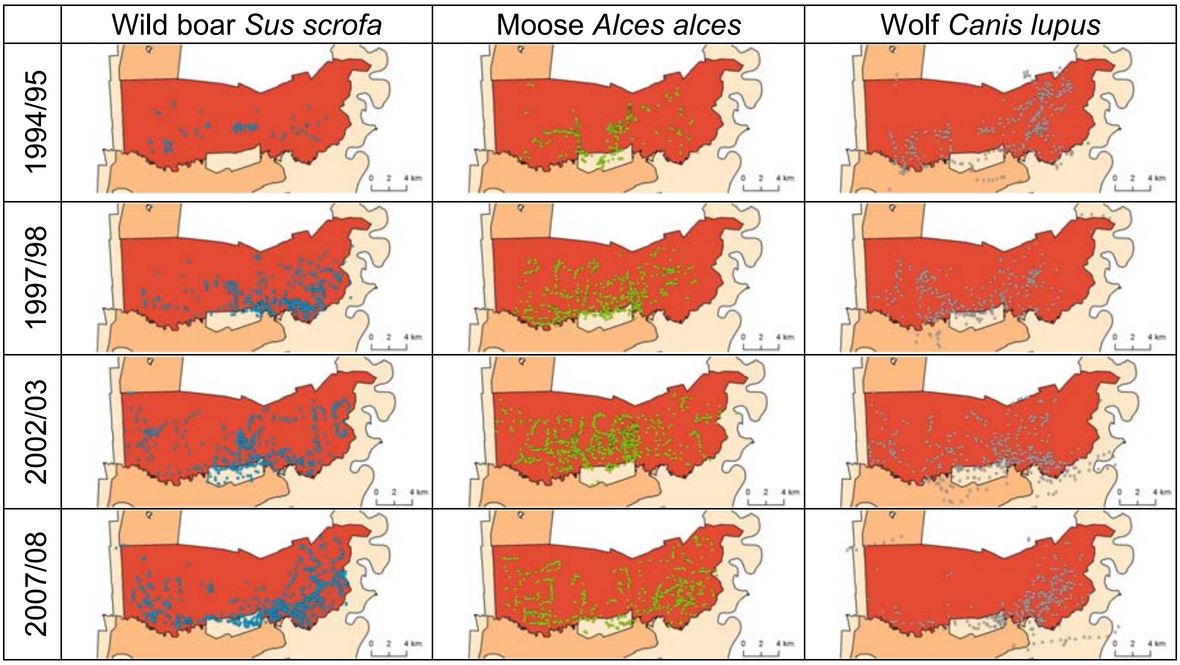
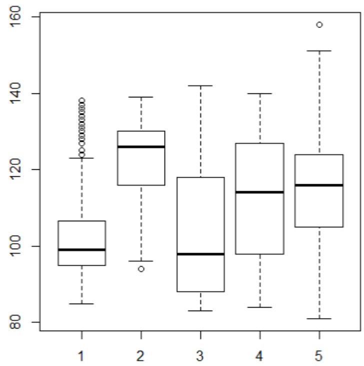
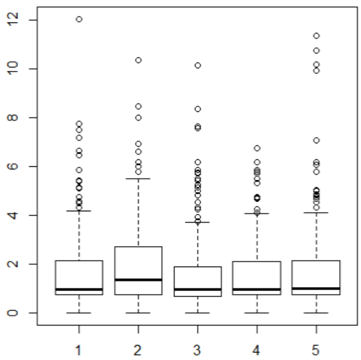
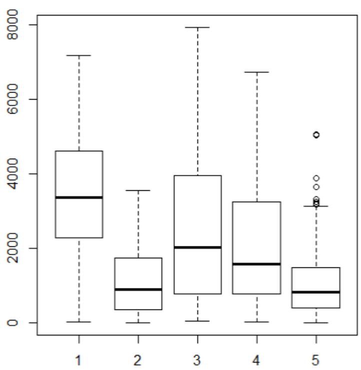
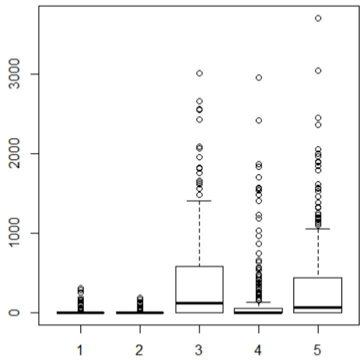
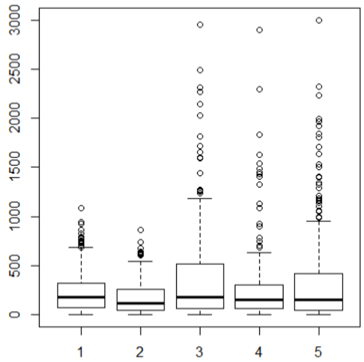
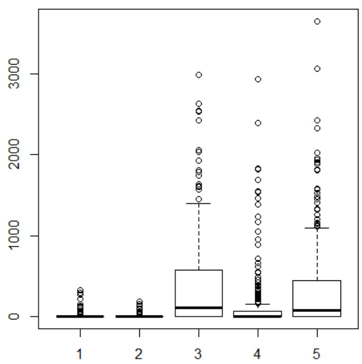
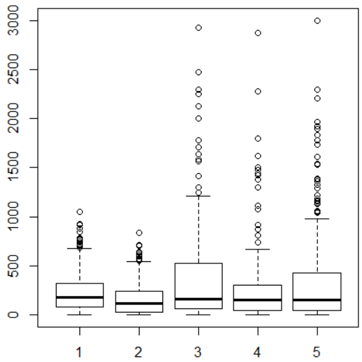
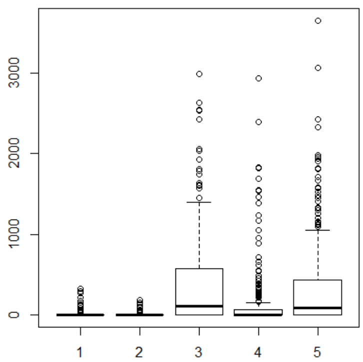
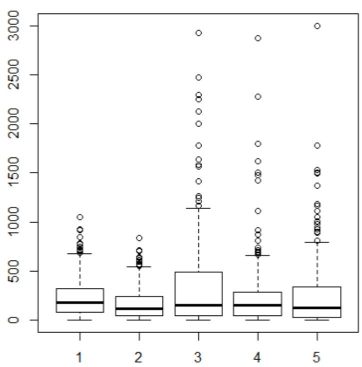
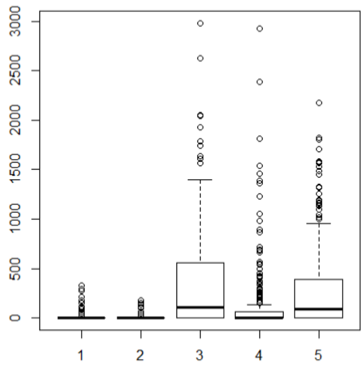
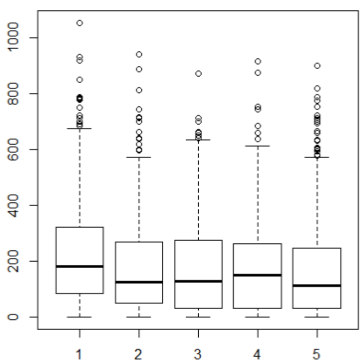
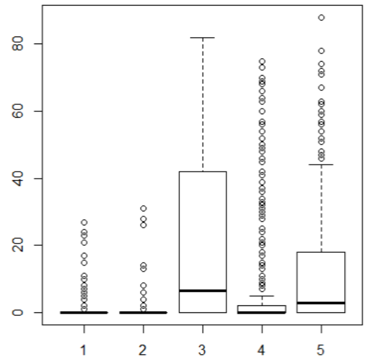
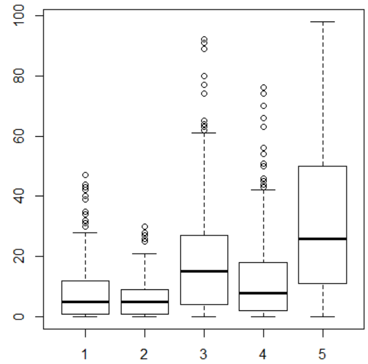
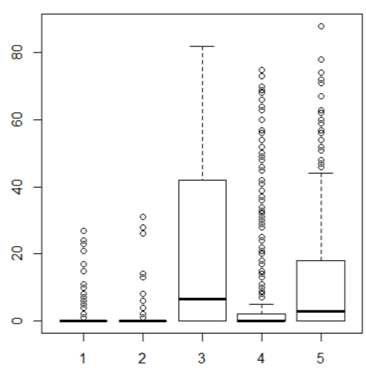
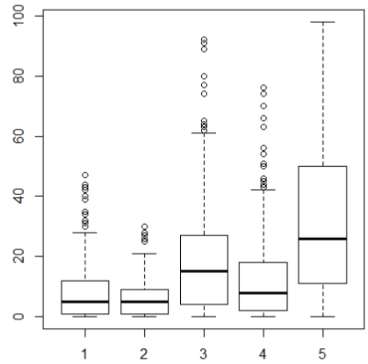
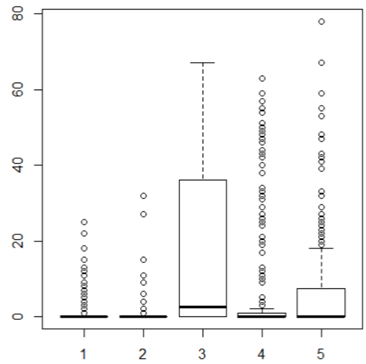
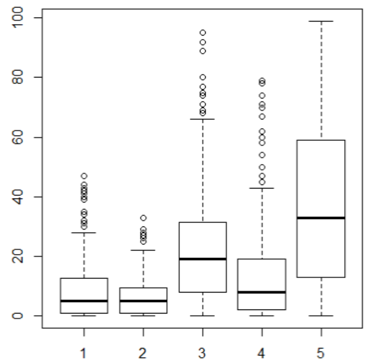
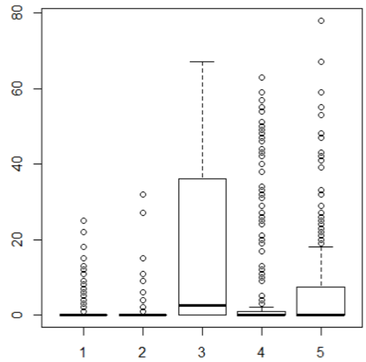
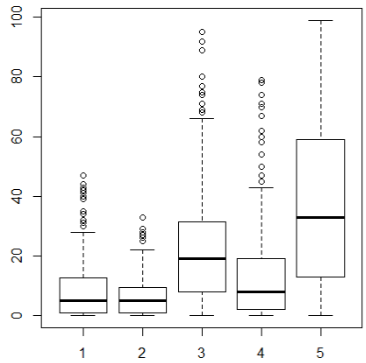


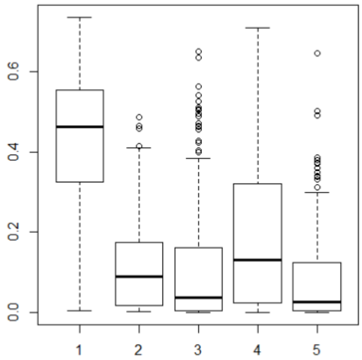
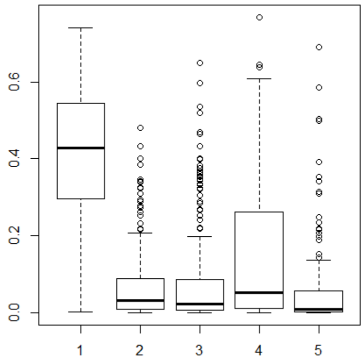
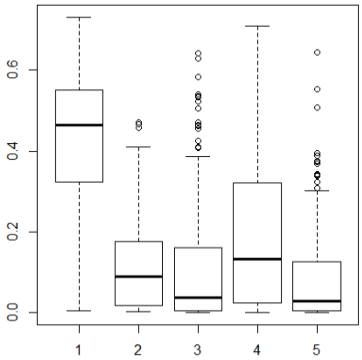
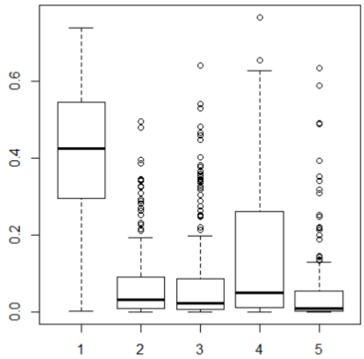
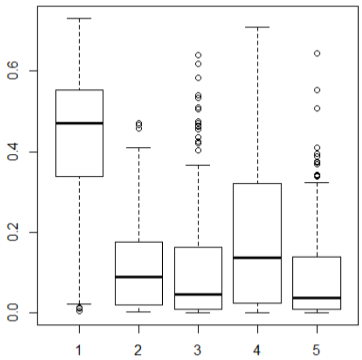
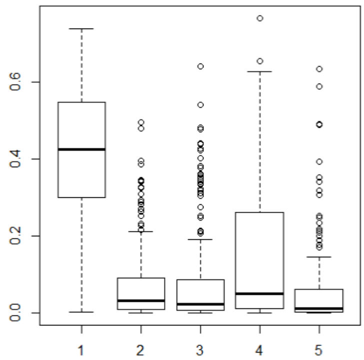
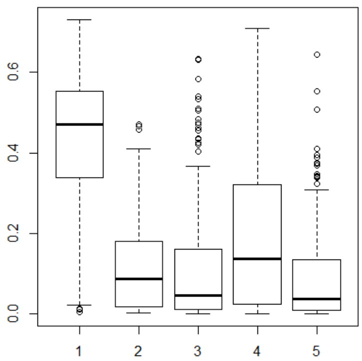
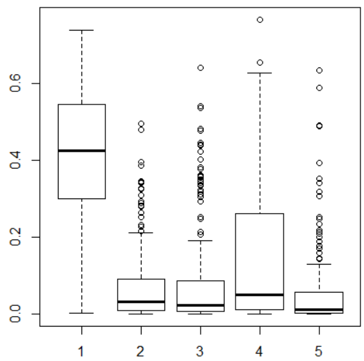
Figure III-S2: Digitized species occurrence points for each of the three species per time step within Oksky State Nature Reserve (dark red = core zone, orange = transition zones, and light red = buffer zone) and its surroundings, collected during the winter (1st October to 31st March).

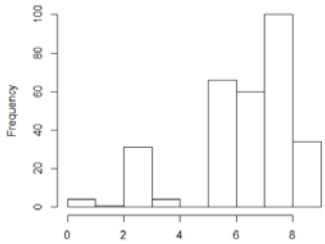
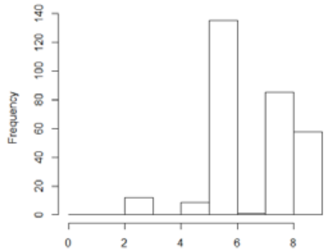
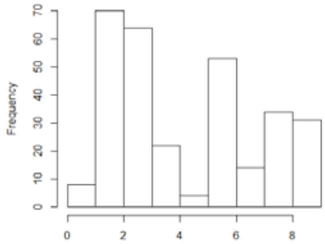
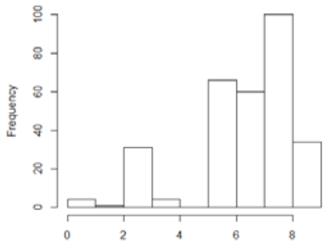
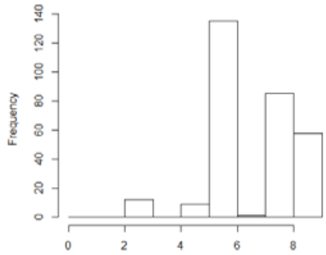
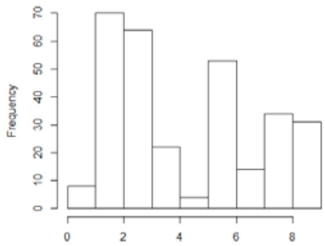
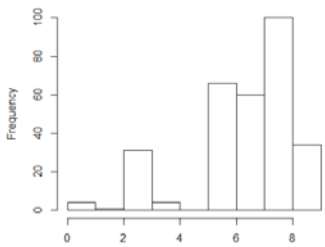
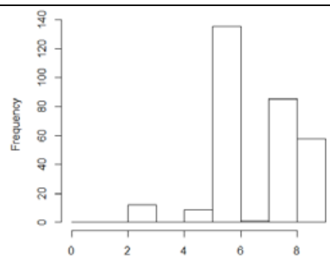
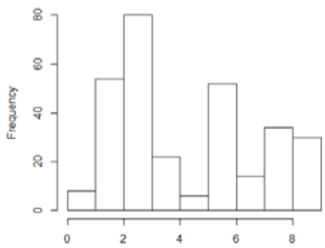
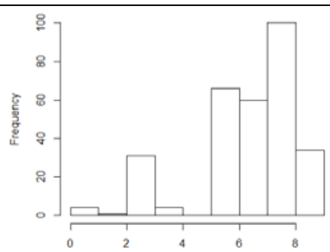
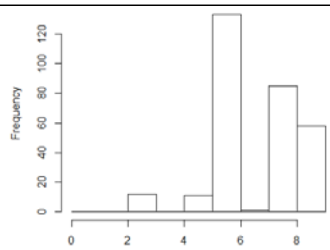
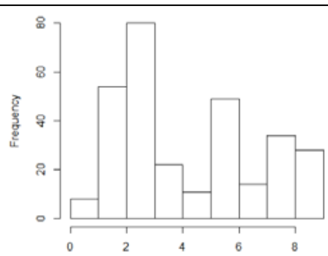
Table III-S1: Descriptive statistics on the environmental conditions in the study area. Boxplot diagrams for random samples (n=300) within five areas of interest within and outside of Oksky State Nature Reserve with 1= core zone, 2 = transition zones, 3 = buffer zone, 4 = entire protected area, and 5 = the 30-km surrounding of the protected area, and histograms for the same random samples for the variable 'land cover' with 1 = Background (water, settlements, roads, clouds, and cloud shadows), 2 = Farmland, 3 = Unmanaged grasslands, 4 = Forest, 5 = Forest disturbances, 6 = Coniferous forest, 7 = Oak-linden forest, 8 = Deciduous forest, and 9 = Mixed forest. The random sample points are associated to the environmental characteristics at each location (See Table III-1).

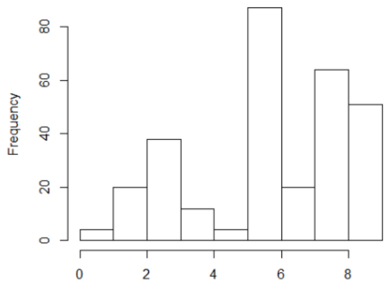
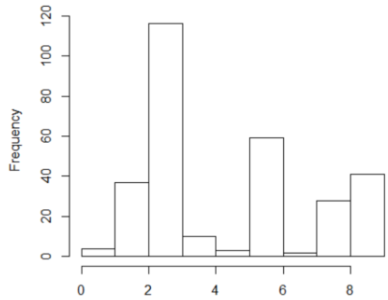
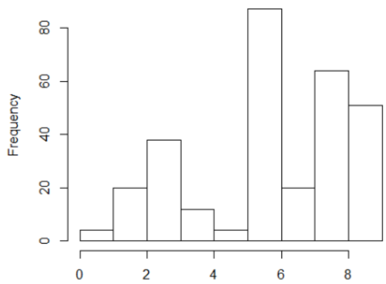
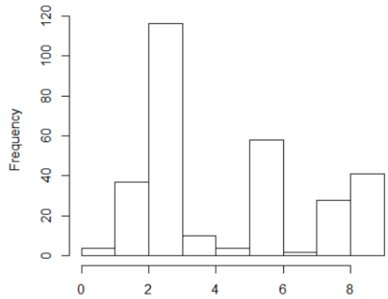
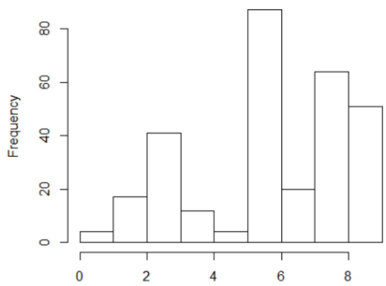
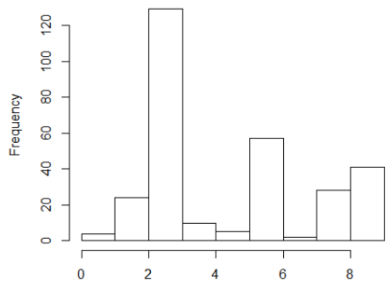
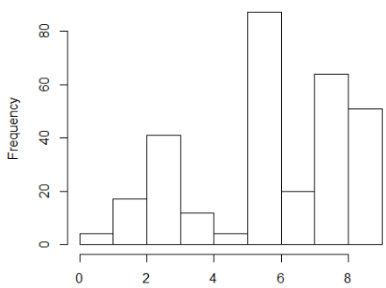
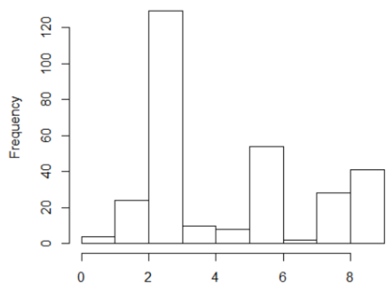
Time-invariant variables	
Elevation [m]	
Slope [°]	
Euclidean distance to roads [m]	

Time-variant variables	Euclidean distance to core forest [m]	Euclidean distance to forest edge [m]
1994		
1997		
2002		
2007		

Time-variant variables	Fraction of farmland [%]	Fraction of grassland [%]
1994		
1997		
2002		
2007		

Time-variant variables	Moose habitat suitability	Wild boar habitat suitability
1994		
1997		
2002		
2007		

	Land cover in the zone of Oksky State Nature Reserve	Land cover in the transition zones of Oksky State Nature Reserve	Land cover in the buffer zone of Oksky State Nature Reserve
1994			
1997			
2002			
2007			

	Land cover in the entire protected area	Land cover in the 30-km surroundings of Oksky State Nature Reserve
1994		
1997		
2002		
2007		

Overview of the results of the time-calibrated species distribution model

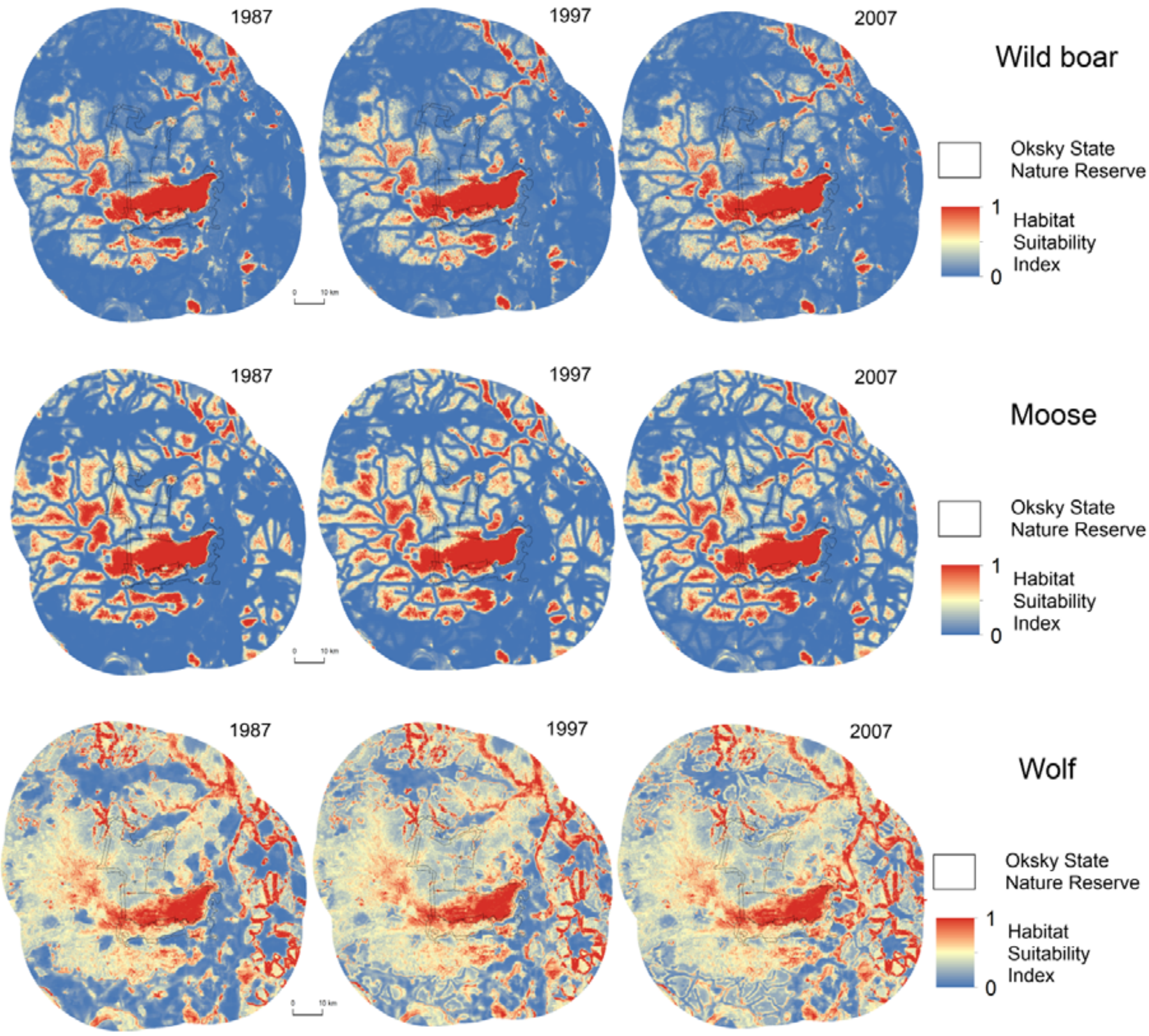


Figure III-S3: Habitat suitability maps for wild boar, moose, and wolf for the years 1987, 1997, and 2007.

Wild boar 1987/2007	**Moose 1987/2007**	**Wolf 1987/2007** (including both prey habitat variables)

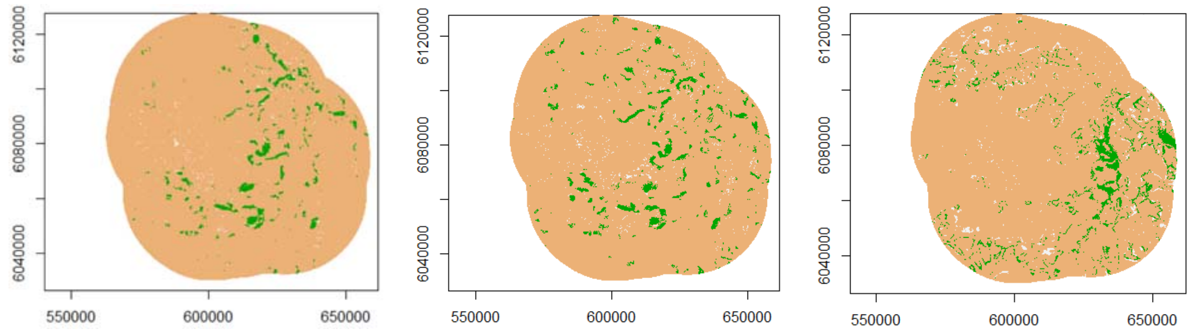


Figure III-S4: Areas of significant changes in predicted habitat between 1987 and 2007. Significance of changes in predicted potential wildlife habitat for wild boar, moose, and wolf between 1987 and 2007. The significance (at the 0.05 level) of pairwise cell-specific differences relative to the mean and variance of all differences between two maps were quantified by applying the SigDiff function available in the R package SDMTools (Bateman et al. 2012; Januchowski et al. 2010). Areas with significant differences were highlighted in a new map. Here, green areas represent where the 1987 model predicts significantly less suitable habitat (standard deviation (SD) < 0.025) than the 2007 model, light grey areas where the 1987 model predicts significantly more suitable habitat (SD > 0.975) than the 2007 model, and areas in apricot define all areas without any significant difference.

Table III-S2: Variable importance in terms of the area under the curve (AUC) for single-variable models, and models with dropped variable for the habitat suitability models of wild boar, moose, and wolf (wolf 1 – including moose habitat and wild boar habitat, wolf 2 – not including any prey variables, wolf 3 – including only wild boar habitat, and wolf 4 – including only moose habitat).

	Wild boar	**Moose**	**Wolf 1**		**Wolf 2**		**Wolf 3**		**Wolf 4**	
Model AUC	0.768	0.734	0.681		0.680		0.681		0.6785	
Variable	AUC single-variable model	AUC single-variable model	AUC single-variable model	AUC dropped variable model	AUC single-variable model	AUC dropped variable model	AUC single-variable model	AUC dropped variable model	AUC single-variable model	AUC dropped variable model
Distance to core forest	0.606	0.559	0.559	0.682	0.559	0.680	0.559	0.681	0.559	0.679
Distance to forest edge	0.550	0.568	0.568	0.682	0.568	0.681	0.568	0.682	0.568	0.679
Elevation	0.698	0.616	0.616	0.677	0.616	0.628	0.616	0.676	0.616	0.670
Slope	0.479	0.505	0.504	0.681	0.505	0.680	0.505	0.681	0.505	0.678
Fraction of farmland	0.597	0.557	0.557	0.682	0.557	0.673	0.557	0.678	0.557	0.678
Fraction of grassland	0.565	0.569	0.569	0.682	0.569	0.679	0.569	0.680	0.569	0.678
Land cover	0.656	0.560	0.560	0.680	0.560	0.668	0.560	0.676	0.560	0.675
Distance to roads	0.606	0.507	0.555	0.680	0.555	0.678	0.555	0.679	0.555	0.677
Moose habitat	x	x	0.650	0.681	x	x	x	x	0.650	0.680
Wild boar habitat	x	x	0.656	0.679	x	x	0.656	0.680	x	x

Table III-S3: Changes in predicted suitable habitat for wild boar, moose, and wolf (including prey habitat variables, and omitting these) in the study area.

	Suitable habitat in study area						*Habitat change*
	1987		*1997*		*2007*		*1987-2007*
	ha	%	ha	%	ha	%	% of 1987' habitat
Wild boar	110,983	15	120,841	16	124,011	17	+12
Moose	314,985	42	359,596	48	387,195	52	+23
Wolf (with prey habitat)	494,367	66	561,857	75	592,744	79	+20
Wolf (no prey habitat)	488,089	65	532,748	71	435,639	58	-11

Chapter IV:
Hunting and land-use change effects on wild boar population dynamics in European Russia during post-Soviet times

Ecological Applications (submitted)

Anika Sieber, Leonid M. Baskin, Alexander V. Prishchepov, Olga V. Goryantseva, Viktor P. Ivanchev, Tatiana A. Markina, Maria V. Onufrenya, Volker C. Radeloff, Nikolai V. Uvarov, and Tobias Kuemmerle

Abstract

Large mammals play crucial roles in ecosystems, yet are globally threatened due to hunting and habitat loss. European Russia provides a unique natural experiment to explore the relative importance of hunting pressure and land-use change for wildlife population because both changed greatly after the collapse of the Soviet Union in 1991. We analysed a 22-year population time series for wild boar *Sus scrofa* from Ryazan Oblast (3.5 million ha) in temperate European Russia versus annual changes in hunting pressure, habitat structure, resource availability, predation pressure, and climate. We applied random effects panel regressions for 1989-2010 and 1999-2010 to assess what affects wild boar population the most. Wild boar populations changed markedly in our study area, with a substantial decline (-81.6%) between 1989 and 1995, a recovery to 1989 numbers by 2003, and a wild boar population in 2010 that was 2.5 times higher than in 1989. Hunting-related variables were significant in all time periods. Whereas factors related to poaching were negatively affecting wild boar populations, the number of officially hunted wild boar was positively and significantly correlated with wild boar numbers. Variables related to habitat structure and resource availability, such as the area of forest, were also significant in our models. Farmland abandonment and changes in forest cover influenced wild boar populations positively after the collapse. Winter harshness was an important determinant throughout time. Our models provide evidence that poaching exerted major pressure on wild boar populations, especially in the 1990s, right after the collapse of the Soviet Union, whereas official hunting did not. We found that humans affected wildlife population trends both through top-down factors, i.e., hunting and poaching, and bottom-up factors, i.e., land-use change. Hunting and poaching, outweighed habitat-related factors by far in our study, suggesting that rewilding opportunities due to declining land-use pressure in the former Soviet Union have to be accompanied by effective enforcement measures to benefit wildlife populations. Our study also underlines the value of long-term wildlife population data to unravel the factors controlling wildlife population dynamics, and the need for continued investment in long-term biodiversity monitoring, such as in Russia.

1 Introduction

Large carnivores and herbivores play critical roles in ecosystems, regulating food webs and providing important ecosystem services such as food, reducing wild fire risks via grazing, and reducing disease outbreaks via predation (Estes et al. 2011). Unfortunately, large carnivores and herbivores are experiencing population declines across the globe (Dirzo et al. 2014; WWF 2014). Hunting and poaching are key top-down causes of these declines, because large mammals often compete with or predate on livestock, are hunted for their meat or trophies, or are persecuted due to human-wildlife conflicts (Dirzo et al. 2014; Ripple et al. 2015). A second major threat to large carnivores and herbivores is habitat loss and fragmentation, affecting these species bottom-up via diminishing resources available to them (Ripple et al. 2014). However, it is not clear which of these two factors is generally more important, and it is crucial for the conservation of large mammals to understand how populations of large carnivores and herbivores respond to top-down vs. bottom-up factors related to human activities.

Hunting pressure and habitat loss do not occur independently from one another. For example, where agriculture expands and roads are built, hunters have easier access (Laurance et al. 2014). Likewise, logging and increasing forest fragmentation lead to higher hunting pressure, for example, in Africa (Laporte et al. 2007) and South America (Lewis et al. 2015). Conversely, where industrialized agriculture expands, marginal farmland is abandoned, and small-holders move away, hunting pressure may decline (Delibes-Mateos et al. 2009). Last but not least, changes in hunting pressure and habitat are often coupled, but they can lead to diverse outcomes, which is why understanding their relative importance is important to develop effective conservation strategies.

Large carnivores and herbivores are not declining everywhere, and especially in the northern hemisphere, their populations are rebounding from past population declines (Chapron et al. 2014), partly due to stricter hunting regulations (Boitani and Linnell 2015). The other main reason for population increases of large mammals have been decreasing land-use pressure and widespread abandonment in Europe (Estel et al. 2015; Kuemmerle et al. 2015) and North America (Ramankutty et al. 2010), which resulted in additional habitat for large carnivores and herbivores (Enserink and Vogel 2006; Ceaușu et al. 2015). However, how large herbivore and carnivore population dynamics have changed in response to these land-use changes, and how important habitat change has been relative to changing hunting pressure, remains weakly understood.

Russia provides a unique 'natural experiment' to study the relative effects of changing habitat and hunting pressure on wildlife populations. After the collapse of the Soviet Union in 1991, Russia experienced drastic changes in socio-economic and institutional conditions, including a major restructuring of agriculture (Lerman et al. 2004). Widespread land-use change occurred in response. Most importantly up to 27 million ha of cropland were abandoned in European Russia between 1990 and 2009 (Schierhorn et al. 2013; Estel et al. 2015). Decreasing livestock numbers were the primary cause of abandonment (e.g., 65% decline in cattle numbers between 1990 and 2010 in Russia; ROSSTAT 2011). Abandoned croplands and pastures provide potential wildlife habitat (Kamp et al. 2015b; Sieber et al. 2015), which may be particularly valuable for large carnivores and herbivores that often have home ranges that are much larger than most protected areas.

At the same time, the collapse of the Soviet Union also resulted in profound changes in socio-economic conditions and game management during the 1990s (Sidorovich et al. 2003), with changing hunting regulations, changes in administrative responsibility, and the privatization of hunting (Braden 2014). The transition period was furthermore characterized by a weakening of institutions, less enforcement of regulations, and reduced funding for nature conservation (Wells and Williams 1998). Finally, the post-Soviet phase entailed severe hardships for Russia's population, as illustrated by a 29% GDP drop and a substantial decline in life expectancy (Stuckler et al. 2009; United Nations Statistic Division 2015), and these hardships were amplified by the financial crises of 1998 and 2008 (Klugman and Braithwaite 1998; Hanson et al. 2012). Together, this resulted in increased poaching in the 1990s and 2000s (Sidorovich et al. 2003), both, for food and trophies, and often of species of conservation concern such as Saiga antelopes (*Saiga tatarica*; Bekenov et al. 1998). Protected areas were important refuges for large mammals during the 1990s and 2000s, even though the effectiveness of protected areas in European Russia was mixed during that time (Wendland et al. 2015), and poaching occurred also inside strictly protected areas (Goodrich et al. 2008).

In summary, both decreasing land-use pressure and more potential habitat, yet also increasing hunting pressure prevailed in the former Soviet Union after 1991, causing in general decreasing wildlife populations in the 1990s and a rebounding thereafter, with substantial variation among species and regions (Bragina et al. 2015a). Fortunately, Russia has monitored large mammal populations extensively since the mid-20th century both inside and outside protected areas (Stephens et al. 2006). These data provide a unique opportunity to understand how the collapse of the Soviet Union affected wildlife population dynamics and to assess the relative importance of hunting pressure and habitat change.

We analysed wild boar *Sus scrofa* population dynamics in European Russia in the post-Soviet period. Wild boar, widespread in Europe and Asia (Melis et al. 2006), are a generalist species and an important game animal in Russia (Baskin and Danell 2003). The main factors driving wild boar mortality are hunting, predation (in European Russia mainly by wolves *Canis lupus*), and starvation during harsh winters (Massei et al. 2015). Specifically, we tested the following hypotheses:

H1: Increased poaching after the collapse of the Soviet Union led to declining wild boar populations,

H2: Increasing official hunting after the institutional and socio-economic transition affected wild boar populations negatively,

H3: Abandonment of arable land led to declining wild boar populations due to reduced forage from crops, and

H4: Abandonment of arable land led to increasing wild boar populations due to increasing habitat area.

2 Methods

2.1 Study area

Our study area covered 21 out of 25 districts (i.e., rayons) of Ryazan Oblast in temperate European Russia (3,477,000 ha; Figure IV-1). Climate conditions are temperate, with an annual mean temperature of 4.2 °C and precipitation of 534 mm (Priklonsky and Tichomirov 1989). Topography is flat with altitudes ranging from 72 to 180 m. North of Oka River are sarmatic mixed forests with spruce *Picea abies* and Scots pine *Pinus sylvestris* and mixed temperate forests with oak *Quercus robur* and marshes. South of Oka River, there are deciduous forests of lime *Tilia cordata* and oak, as well as open steppe and arable land.

Agriculture is widespread, including cultivation of summer and winter crops and livestock farming. During Soviet times, agricultural land was mainly managed by the state and heavily subsidized (Prishchepov et al. 2013). Until 1991, 46% of the study area was agricultural land (i.e., arable land and pastures), 30% forests, and 18% unmanaged grassland (Sieber et al. 2013). After 1991, rural population declined from 465,806 citizens in 1990 to 342,525 citizens in 2010 (-36%; RYAZANSTAT 2010), and unemployment rates increased from 0.01% in 1991 to 8.4% in 2010 (ROSSTAT 2015).

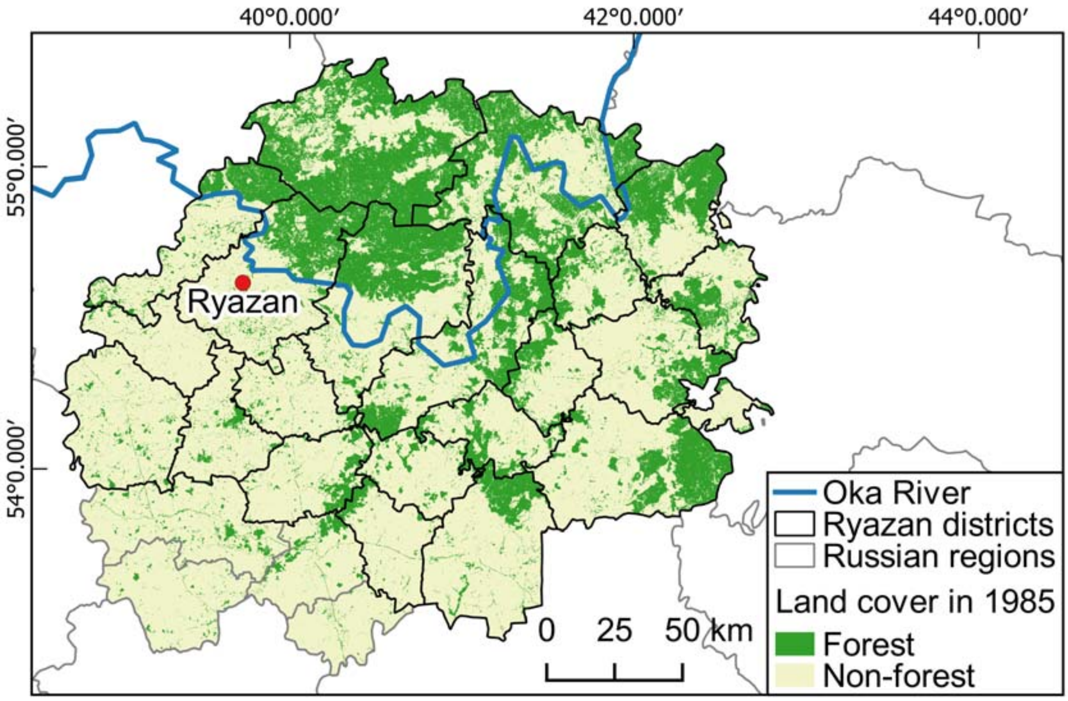


Figure IV-1: Study area in temperate European Russia with Ryazan City in Ryazan Oblast and forest cover in 1985 (forest cover in 1985 based on (Potapov et al. 2015) and (Sieber et al. 2013)).

About 40% of the agricultural land in 1988 was abandoned by 2010 (Sieber et al. 2013), livestock numbers declined greatly (-75%, -78%, and -87% from 1990 to 2007 for cattle, pigs, and sheep; ROSSTAT 2008). On abandoned areas, natural succession is widespread and about 9% already reverted back to forests (Sieber et al. 2013). Furthermore, substantial changes in forest management occurred, logging decreased in the early 1990s to very low rates, and only recovered to about half of the late-Soviet logging rates in the 2000s (about 0.2%; Sieber et al. 2013).

Ryazan Oblast has a diverse community of large mammals, including wolf, moose *Alces alces*, and wild boar. Wild boar is an important game animal and was reintroduced in the 1960s (Pankova 2013) after extirpation in the 18th century. Game populations are annually monitored in order to set hunting limits and quotas (Avdeev et al. 2015). In 2014, hunting was allowed on about 3,286,000 ha (83% of the total area of Ryazan Oblast), including both private and public hunting grounds (Avdeev et al. 2015). Both hunting quotas issued and the number of wild boar harvested increased during the 2000s (Tsarev 2007; Volodina 2010). In our study area, there are eleven protected areas (IUCN categories Ia-IV), with Oksky State Nature Reserve (founded in 1936) and Meshchersky National Park (1992), together covering about 468,500 ha (11.8% of Ryazan Oblast). In these federal protected areas, hunting is prohibited with few exceptions (No. 33-FZ Federal law on specially protected natural areas, 1995).

2.2 Data

2.2.1 Species data

In Russia, annual estimations of species' populations are dominantly based on standardized winter track counts, where animal tracks on fresh snow are counted along fixed transects (Bragina et al. 2015a), and abundance is estimated using the Formozov-Malyshev-Pereleshin formula, which includes species-specific estimates of daily travel distances (Stephens et al. 2006). We acquired abundance data for wild boar and wolf (the main predator of wild boar) for each of the 21 districts of Ryazan Oblast from the Ministry of Natural Resources and Ecology of Ryazan Oblast (further Ministry) and the Russian Federal Agency of Game Mammal Monitoring (FGBU "Tsentrohotkontrol"). The abundance data covered the period 1981-2013 for wild boar and 1994-2013 for wolf, and since 2008, the Ministry has excluded all data from three protected areas (Oksky State Nature Reserve, Meshchera National Park, and Ryazansky Zakaznik), which did not change the population trends in the dedicated districts.

We homogenized the data in three steps. First, we merged the two data sets and calculated the average if there were two values for a given year. Years without a record in either dataset were labelled as 'no data' (1% of the wild boar data in 1989-2010, and 39% of the wolf data in 1999-2010). Second, we interpolated 'no data' values using a cubic spline interpolation (using the R package splines), or mean values or prior and subsequent year when the cubic spline interpolation resulted in negative numbers. For data gaps at the beginning of the time series we used linear extrapolation (for one district only). Third, we computed the rolling mean of three observations (using the R package zoo, k=3) to dampen outliers (Kamp et al. 2015a; Figure IV-2).

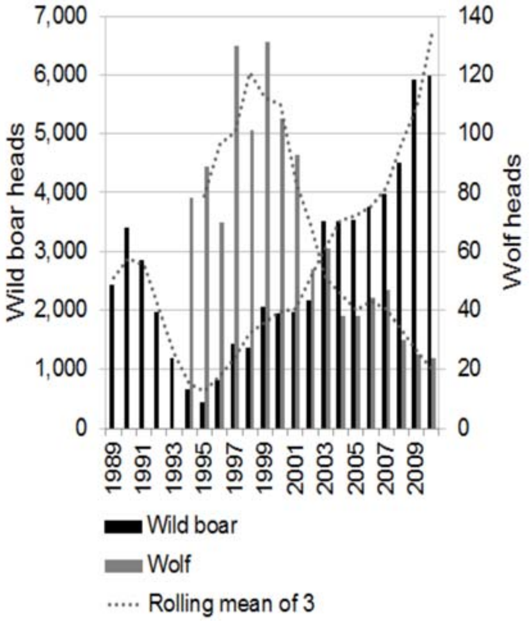


Figure IV-2: Population dynamics of wild boar (1989-2010) and wolf (1994-2010) in the study area of Ryazan Oblast, with original number of animal heads in bars and smoothed data with a rolling mean of three observations in dotted lines.

2.2.2 Environmental characteristics

To explain wild boar population dynamics, we selected predictor variables based on a literature review and expert knowledge on the species ecology and the region (six of our co-authors have worked as ecologists in the region for decades), which proxy (1) hunting pressure, (2) habitat structure and resource availability, and (3) natural mortality of wild boar (Table IV-1). For hunting pressure, we included two proxies of poaching that is the total human rural population and the protected area extent, and one variable capturing official hunting with the number of hunted wild boar. Regarding habitat and resource availability, we included the extent of forest, arable land and unmanaged grassland as proxies for the supply of forage and shelter, and acorn productivity in the previous year as a proxy for resource availability (Borowik et al. 2013; Dorresteijn et al. 2015; Morelle and Lejeune 2015). Regarding control variables on factors contributing to mortality other than hunting, we included wolf abundance to proxy predation, and mean January temperature and maximum snow depth as proxies for winter harshness (Baskin and Danell 2003; Melis et al. 2006). For all variables, we analysed absolute values as predictors of absolute numbers of wild boar (Figure IV-3).

Table IV-1: Predictors of wild boar population dynamics in Ryazan Oblast (Spatially invariant data refer to time-series data at Ryazan Oblast level, all other at district level, i.e., 21 districts).

Variable	Characteristics	A-priori assumption	Data source
Hunting pressure			
Total human rural population	1989-2010; individuals	Low rural population size serves as a proxy for low human impact (i.e., hunting/poaching) and leads to lower wild boar mortality	(RYAZANSTAT 2010)
Protected area	Summed extent of all protected areas (IUCN categories Ia-IV; since 1994 maximum extent); 1989-2010; ha	High protected area extent leads to lower wild boar mortality	(IUCN and UNEP-WCMC 2014); Oksky State Nature Reserve; www.oopt.info
Number of hunted wild boar	1999-2010; spatially invariant; heads	High number leads to higher wild boar mortality, but depends on sustainability of game management and wild boar fertility	(Lomanov 2000, 2004; Tsarev 2007; Volodina 2010)
Habitat structure and resource availability			
Forest area	Coniferous, deciduous, and mixed forest; proxy of supply with forage and shelter; 1989-2010; ha	High fraction of forest area provides forage and shelter and leads to lower wild boar mortality	(Sieber et al. 2013)
Arable land	Time series of sown area, proxy of forage supply; 1989-2010; ha	Large area of arable land provides forage and leads to lower wild boar mortality	(RYAZANSTAT 1990-2010)
Abandoned arable land 1989-98	Difference in sown area between 1989 and 1998; 1999-2010; ha	Large area of abandoned arable land leads to higher wild boar mortality	(RYAZANSTAT 1990-2010)
Unmanaged grassland	Area of unmanaged grassland, proxy for undisturbed habitat; 1989-2010; ha	Large area of unmanaged grassland results in decreasing human disturbance and more potential wild boar habitat	(Sieber et al. 2013)
Gain of unmanaged grassland 1989-98	Difference in the area of unmanaged grassland between 1998 and 1989; 1999-2010; ha	Large gain of unmanaged grassland leads to lower wild boar mortality	(Sieber et al. 2013)
Acorn	Harvest of *Quercus*	High harvest of acorns	Chronicles of Nature of

productivity	*robur L.* on a constant phenological route and visual assessment according to V.G. Kapper (1930) in the previous year; 1989-2010; spatially invariant; 0.0-5.0 points	leads to lower wild boar mortality	Oksky State Nature Reserve 1989-2010, Total amount XLI-LXII, Scientific library of Oksky State Nature Reserve, Russia
Natural mortality			
Wolf abundance	Main predator; 1999-2010; rolling mean of three observations; heads	Higher wolf abundance leads to higher predation and higher wild boar mortality	Ministry of Natural Resources and Ecology of Ryazan Oblast, Russia
Mean January temperature	Proxy of winter harshness (Melis *et al.* 2006); 1989-2010; spatially invariant; °C	Harsh winters lead to higher wild boar mortality	(Onufrenya 2003, 2012)
Maximum snow depth	Proxy of winter harshness; 1989-2010; spatially invariant; cm	High snow depth impedes digging for food and leads to higher wild boar mortality	Chronicles of Nature of Oksky State Nature Reserve 1989-2010, Total amount XLI-LXII, Scientific library of Oksky State Nature Reserve, Russia

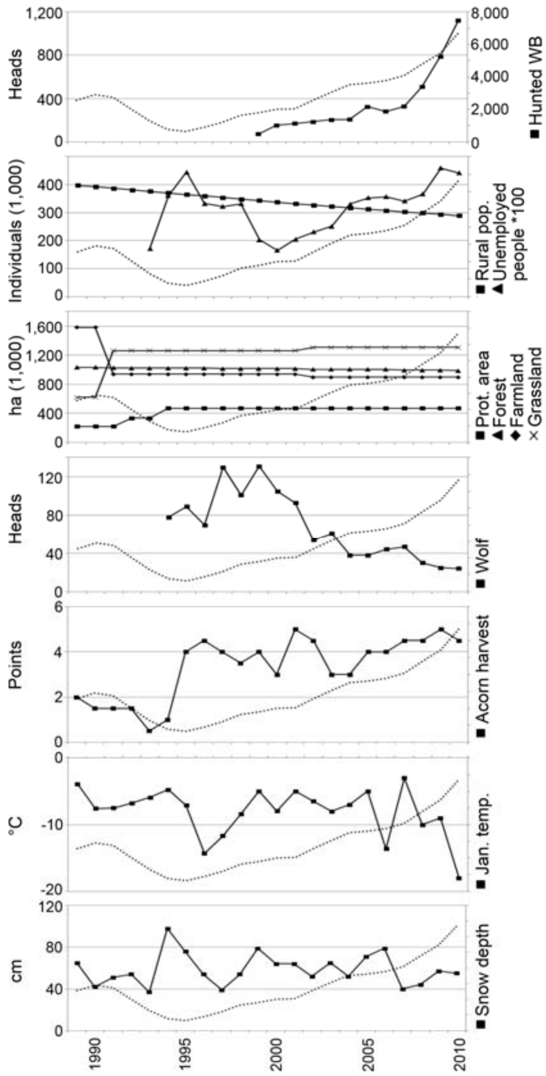


Figure IV-3: Changes in predictor variables (primary y-axes) and wild boar population size (secondary y-axes, rolling mean of three observations in dotted lines) 1989-2010.

2.3 Panel regression model

To assess the drivers of wild boar population dynamics in our study area, we carried out two analyses. First, we calculated Spearman correlation coefficients to explore the relationship between the wild boar numbers in Ryazan Oblast between 1989/1999 and 2010 and our predictor variables. Second, we applied panel regression using the R package plm to test our four hypotheses. Panel regressions allow for assessing the impact of time-variant and time-invariant predictors on a phenomena of interest, while controlling for unobservable effects or missing data (Baltagi 2005; Croissant and Millo 2008). Not all our variables were available for the full time period 1989-2010, and we therefore fitted two panel models, one for 1989-2010 and one for 1999-2010 (Table IV-2). The 1999-2010 model fitted an unbalanced panel, i.e., a varying number of cross-sectional observations over time (Croissant and Millo 2008), because of missing data for several predictors in certain years. Because we were interested in the effects of both static and time-variant variables, we fitted random effects models to include time-invariant variables (Greene 2012):

$$Y_{it} = \alpha + ßX_{it} + u_i + \varepsilon_{it} \qquad (1)$$

where Y_{it} is the dependent variable in district (entity) i at time t, α the unknown intercept, ß the estimated coefficient of X, X_{it} the predictor variable in district i at time t, u_i the time-constant between-entity error, and ε_{it} the within-entity error (Torres-Reyna 2007; Greene 2012).

We assessed model performance using the adjusted R-squared. Furthermore, we tested for heteroscedasticity (i.e., whether model errors (ui and εit) varied across districts and time; Baltagi 2005) by applying the Breusch-Pagan test, and for temporal autocorrelation using the Breusch-Godfrey/Wooldridge test. We found both heteroscedasticity and temporal autocorrelation, which may lead to decreased standard errors, and applied the Arellano robust covariance matrix estimator (Arellano 1993; Baltagi 2005) to adjust standard errors and significance values.

3 Results

3.1 Wild boar and wolf dynamics in Ryazan Oblast

The wild boar population in our study area changed markedly from 1989 to 2010 (Figure IV-2). After the collapse of the Soviet Union in 1991, wild boar numbers plummeted from 2,860 in 1991 to 445 animals in 1995, but they recovered to the 1991 level by 2003, and rose to 5,984 animals by in 2010. Population trends were similar in all districts (Supporting Information). The wolf population changed also considerably from 1994 to 2010 (Figure IV-2), increasing strongly from 78 in 1994 to 131 animals in 1999. In the 2000s, wolf numbers decreased to only 24 in 2010 (0.3 times the population of 1994) and wolves were absent in nine districts (Supporting Information).

3.2 Factors shaping wild boar population dynamics in Ryazan Oblast

Univariate correlations of wild boar numbers with our predictors were generally of moderate strength (Figure IV-4), and weak for the hunting pressure variables (maximum r = 0.28, with rural population, 1989-2010; and 0.38, with number of hunted wild boar, 1999-2010). Correlation with the variable set of habitat structure and resource availability was also weak except for forest, which was moderately correlated (max. r = 0.57) in 1989-2010 and strongly correlated (max. r = 0.68) in 1999-2010. Collinearity among predictor variables was also generally weak, with the exception of rural population and the area of unmanaged grassland in 1989-2010 (r = 0.64), and forest area and wolf numbers in 1999-2010 (0.67, Figure IV-4).

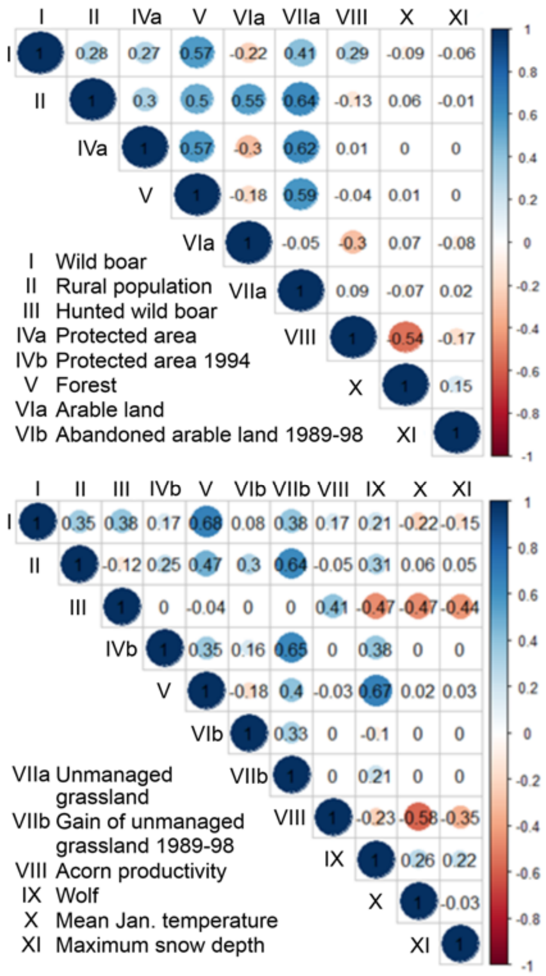


Figure IV-4: Spearman correlation coefficients between wild boar abundances and all predictor variables of the two different variable sets (top: 1989-2010 model, bottom: 1999-2010 model).

However, while univariate relationships were weak, many variables were highly significant in our multivariate models. For example, in the model for 1989-2010, variables from all three groups, hunting pressure, habitat, and natural mortality, were significantly related to wild boar population trends. The protected area extent, which increased until 1994 (Figure IV-3), was highly significant ($p<0.001$) and influenced wild boar numbers negatively (Table IV-2). Rural population, which decreased, also negatively influenced wild boar populations ($p<0.1$). In terms of habitat-related variables, forest area, which slightly decreased, was significant ($p<0.01$) and positively related. Arable land, which decreased, significantly ($p<0.01$) was negatively related. Conversely, unmanaged grassland area, which increased, was positively related ($p<0.01$). Lastly, maximum snow depth was highly significant ($p<0.001$) and negatively related, as was mean January temperature ($p<0.01$; Table IV-2).

Table IV-2: Results of the random effects panel regressions evaluating wild boar population dynamics in Ryazan Oblast for two different panels showing the estimated coefficients of the predictor variables with adjusted standard errors, model performance measures, and model specifications.

Predictor variables	1989-2010 model ß	1989-2010 model Std. error		1999-2010 model ß	1999-2010 model Std. error	
Intercept	103.68	46.675	*	-2.3216	45.454	
Rural population [individuals]	-0.0029	0.0016	.	-0.0034	0.0019	.
Protected area [ha][a]	-0.0013	0.0004	***	-0.0007	0.0006	
Hunted wild boar [heads]	--	--		0.1918	0.0504	***
Forest area [ha]	0.0017	0.0006	**	0.0022	0.0003	***
Arable land [ha]	-0.0019	0.0007	**	--	--	
Abandoned arable land 1989-98 [ha][b]	--	--		0.0030	0.0022	
Unmanaged grassland [ha]	0.0016	0.0006	**	--	--	
Gain of unmanaged grassland 1989-98 [ha][b]	--	--		0.0029	0.0018	
Acorn productivity [points]	5.2300	4.9024		-9.9270	3.9468	*
Wolf abundance [heads]	--	--		-0.0913	2.4557	
Mean January temperature [°C]	-5.3617	1.9556	**	-2.3747	0.7490	**
Maximum snow depth [cm]	-1.1100	0.2991	***	-1.1792	0.3225	***
R^2	0.306			0.434		
Adjusted R^2	0.300			0.413		
Number of total observations (N)	441			234		
Number of districts (n)	21			21		
Years (T)	21			3-12		
Number of districts per time period	1989-2010: 21			1999-2010: 19 2008-2010: 2		
Panel	Balanced			Unbalanced		

*Significance levels: . p<0.1; * p<0.05; ** p<0.01; *** p<0.001*
ß: estimated coefficient
[a]Summed extent of protected area per year in the 1989-2010 model (time-variant); maximum extent of protected area (reached in 1994) in the 1999-2010 model (time-invariant)
[b]Time-invariant variables summarizing the area change in the time period 1989-98

In our 1999-2010 model, fewer variables influenced wild boar numbers, but the signs of our variables remained largely unchanged (Table IV-2). Variables related to hunting pressure were again important. Rural population size, a proxy of poaching, was again significant ($p<0.1$) and negatively related. In contrast, official offtake (i.e., number of hunted wild boar), which was increasing over time, had a positive and highly significant ($p<0.001$) effect. Regarding variables related to habitat structure and resource availability, forest area ($p<0.001$) had a positive sign, as in the 1989-2010 model. Acorn productivity became an important variable ($p<0.05$), whereas the extent of abandoned arable land during the period 1989-98, and the grassland gain during that period, were not significant.

Regarding factors related to natural mortality, wolf abundance was unimportant in our model, while the two climate variables remained important, as in the 1989-2010 model (Table IV-2). Both panel regression models resulted in reasonable model fit, explaining about 30% and 41% of the total variance in in 1989-2010 and 1999-2010, respectively (Table IV-2).

4 Discussion

Understanding the relative effects of direct human pressure versus changes in habitat on large carnivores and herbivores is important for developing effective conservation measures. Here, we analyzed a time series of wild boar populations from European Russia for 1989-2010, when the collapse of the Soviet Union provided a unique 'natural experiment' due to major changes in land use and socio-economic and institutional conditions. Using panel regressions, we assessed the importance of variables capturing official hunting, poaching, and habitat change, while controlling for natural drivers of wild boar population.

We found substantial support for our first hypothesis, that poaching affected wild boar number negatively. Our proxies for poaching, i.e., rural population and protected area extent, were consistently negatively related to wild boar abundance, and the decreasing rural population in our study area (Ioffe et al. 2004) affected wild boar positively, likely because fewer rural residents meant reduced subsistence poaching. This is similar to other regions in Europe, although the total number of hunters in European Russia remained constant after 1990 (Massei et al. 2015). The protected area extent affected wild boar negatively in 1989-2010, likely for two reasons. First, while protected areas have been effective in curbing deforestation (Sieber et al. 2013; Wendland et al. 2015), they may not always curb poaching (Redford 1992; Wilkie et al. 2011). Second, the establishment of new protected areas in the study region, such as the expansion of Oksky State Nature Reserve in 1989 and the Ramsar Site of Oka and Pra River Floodplains in 1994 occurred during times of declining populations of wild boar and other large mammal species (Bragina et al. 2015a).

We did not find support for our second hypothesis that official hunting decreased wild boar population, although wild boar is an important game animal in Russia and official data showed a strong increase in hunting of wild boar after 1999 (3% of the wild boar population were hunted in 1999 versus 18% in 2010, Figure IV-2). We suggest that the surprising positive relationship between official hunting harvests and wild boar population is because hunting quotas rose as population increased. Indeed, hunting quotas were often not reached in Ryazan Oblast, at least in the period 2005-2010 (Tsarev 2007). Unfortunately, official hunting statistics are not capturing poaching, a major cause for diminishing wildlife populations in Russia in the 1990s (Bragina et al. 2015a). Indeed, the effect of poaching must have been quite substantial before 1999, given that large numbers of wild boars were harvested after 1999 without detrimental effects on the population growth rate and socio-economic conditions in Russia only improved after 1998 (Hanson 2009). In addition, wild boar reproduction rates increase as hunting pressure increases, which makes wild boars hard to control via hunting (Servanty et al. 2011).

Our second pair of hypotheses suggested that post-Soviet land-use change, particularly farmland abandonment, impacted wild boar populations either negatively, via reduced forage from arable land or, positively, by providing additional habitat on abandoned farmland. In our models, the area of arable land was negatively affecting wild boar trends in the 1989-2010 model, which is surprising given that wild boar forages in agricultural fields, especially during the growing season (Herrero et al. 2006; Fonseca 2008). This may be because wild boar prefers agricultural fields close to a forest edge (Thurfjell et al. 2009), which were largely abandoned in our study area (Sieber et al. 2013). However, based on our model, we rejected our hypothesis that reduced forage availability affected wild boar negatively. In contrast, the area of unmanaged grassland was positively related to wild boar numbers in the 1989-2010 model, thus providing support for our hypothesis of increasing habitat availability. The post-1991 collapse of agricultural systems in Ryazan Oblast resulted in widespread abandonment of former cropland and pastures, which provided new potential habitat for wild boar (Sieber et al. 2015). However, habitat variables related to farmland abandonment were of less importance than hunting-related variables, which might be caused by the time lag of impacts due to habitat changes compared to those related to poaching.

Winter harshness was an important determinant in our models and affected wild boar generally negatively. The negative relation with the mean January temperature was unexpected though. In general, mild winters were favouring wild boar abundance in Europe in recent years (Melis et al. 2006; Massei et al. 2015). Wolf abundance was not significantly related to wild boar populations in our 1999-2010 model. Given the fairly low number of wolves in our study region due to disease (Pozio et al. 2001), hunting (Sidorovich et al. 2003), and extirpation programs (Sastre et al. 2011), and the strong increase in wild boar populations observed in our study period, this may have masked a predation effect, because wolf is one of the main predators of wild boar in Eurasia (Baskin and Danell 2003) and is usually limiting ungulate densities (Jedrzejewski et al. 2002).

While our study used a unique, long-term data set on wild boar abundance and a rich suite of predictor variables, and our panel models explained the majority of the variance, we encountered a few limitations. First, winter track counts were not conducted continuously during the 1990s (Fiorino and Ostergren 2012; Supporting Information). Second, outside the protected areas, winter track counts are gathered by hunters themselves. Although hunters are usually interested in sustainable game management (Baskin 2009), intentional misrepresentation of either wild boar abundance or the number of hunted animals cannot be ruled out. However, given that hunting quotas have often not been met, there would be little incentive to underreport either. Third, data on wolves are difficult to gather because these animals are elusive, due to decades of severe persecution (Gubar 2010). Our wolf numbers may thus be conservative. Finally, missing data in some of our predictor variables resulted in an unbalanced panel, which prohibited accounting better for spatial autocorrelation by using the econometric model for spatial panel data (R package splm; Millo and Piras 2012).

5 Conclusions

Our study provides evidence that human affected wildlife population trends both via top-down effects, such as poaching, and bottom-up effects, such as land-use and resulting habitat change. We found that wild boar population trends after the collapse of the Soviet Union were negatively affected by poaching and positively affected by habitat gain due to farmland abandonment. Factors related to poaching outweighed habitat-related factors, particularly those describing farmland abandonment, in our study. This means that rewilding opportunities stemming from additional wildlife habitat due to abandoned farmland in the former Soviet Union (Sieber et al. 2015), will need to be accompanied by enforcement measures to control poaching. Our study also underlines the value of long-term wildlife population data to unravel the factors controlling wildlife population dynamics, highlighting the need for continued investment in biodiversity monitoring where long-term data are collected, such as in Russia.

Acknowledgements

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Supporting Information

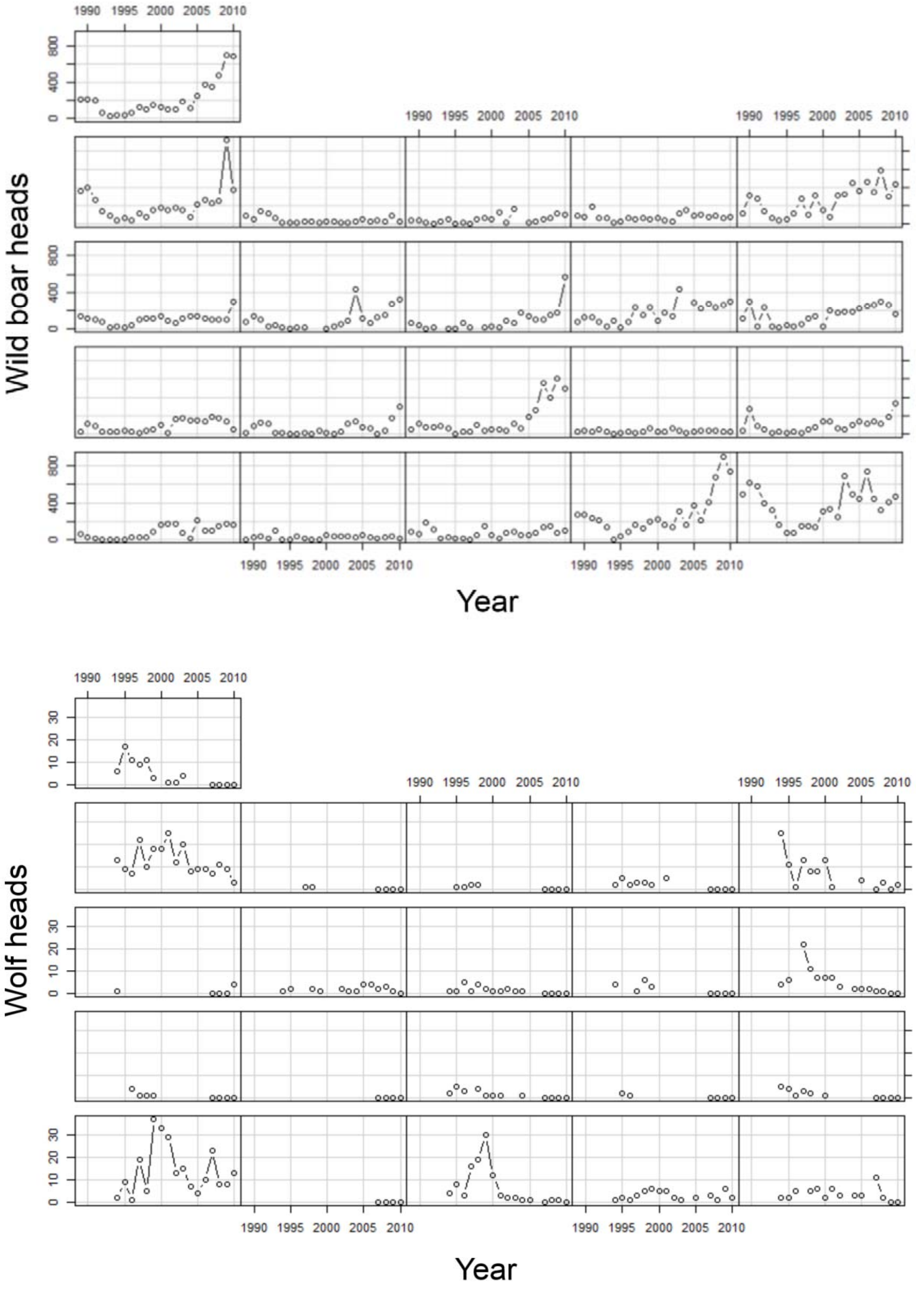

Figure IV-S1: Numbers of wild boars *Sus scrofa* and wolves *Canis lupus* (original data) in 21 districts of Ryazan Oblast, 1989-2010 (data source: Ministry of Natural Resource and Ecology of Ryazan Oblast, Russia).

Chapter V:
Synthesis

1 Summary

The overall aim of this thesis was to contribute to a better understanding of how the socio-economic and institutional shock of the breakdown of the Soviet Union in 1991 affected land use, protected area effectiveness, and wildlife dynamics in European Russia. The breakdown of the Soviet Union was a rapid shock in socio-economic and institutional conditions that certainly affected the way in which humans impact protected and unprotected habitats and wildlife dynamics, in particular regarding land use and hunting. However, current knowledge on how changes in land use and hunting pressure triggered by the breakdown of the Soviet Union were interrelated and which consequences arose for wildlife and nature conservation in post-Soviet European Russia is limited.

This thesis applied different approaches to address these knowledge gaps. Rates and spatial patterns of post-Soviet land-use change in temperate European Russia were quantified and allowed characterizing the temporal and spatial variability of different processes in the study area. Based on these results, the effectiveness of protected areas in preventing forest-cover loss was determined, complemented by the identification of changes in large mammals' habitat within protected and unprotected areas. The temporal dynamics of large mammals' populations were evaluated and the most important drivers and their relative importance were identified. Findings of these analyses were used to answer the three overarching research questions of this thesis.

Research question I: *How did the breakdown of the Soviet Union affect land use in European Russia?*

Chapter II aimed at mapping spatial and temporal patterns of post-Soviet land-use change in temperate European Russia and identified changes in farmland and forest cover. Particularly, farmland abandonment and changes in forest cover due to both natural succession on abandoned farmland and forest disturbances were mutually assessed to answer this research question.

Chapter II showed that land-use change was substantial and widespread in temperate European Russia. About 40% of the farmland managed in the late 1980s was abandoned until 2010. Abandoned farmland transitioned into grassland, shrubland, and juvenile forests, especially on marginal land close to forests.

Chapter II also showed that forest cover changed within the 27-year study period. First, about 5% of the total forest area was disturbed, mainly due to logging. Annual disturbance rates showed a distinct temporal trend with an initial decline of forest logging rates from about 0.5% in the late Soviet era to a low of about 0.1% in the 1990s, and increasing again to only about half of the rates of the late Soviet era in the 2000s. Second, at the same time, forest cover partially increased again, mainly due to natural succession on abandoned farmland and regrowth on previously disturbed forest areas. In 2010, forest covered about 9% of the abandoned farmland, representing a conservative estimate though due to the time-lagged effect of natural succession.

In summary, the breakdown of the Soviet Union vastly affected land use in European Russia by reducing land-use pressure due to farmland abandonment and overall lowered rates of forest logging. Reduced land-use pressure and natural succession on abandoned farmland, particularly on marginal land, initialized rewilding trends in the broader landscape.

<u>Research question II</u>: *How effective have protected areas been in post-Soviet European Russia?*

Chapter II and III aimed at evaluating the effectiveness of protected areas in temperate European Russia. Particularly, the focus was on determining the relative effectiveness of protected areas in preventing forest disturbances within their territory compared to their surroundings, and on identifying changes in the habitat availability of large mammals due to post-Soviet land-use change within and outside protected areas.

Chapter II showed that two strictly protected areas, i.e., Oksky and Mordovsky State Nature Reserves, were overall effective in limiting forest logging within their territories. Both protected areas showed lower forest disturbance rates and lower probabilities of experiencing forest disturbance within their boundaries compared to the surroundings throughout the entire study period 1986-2010. Forest disturbance rates were lowest in those protection zones with the highest possible protection status and increased towards other protection zones and the surrounding areas. Reduced land-use pressure due to lowered forest-logging rates in the protected area surroundings in the post-Soviet period resulted in the declining effectiveness of strictly protected areas over time.

Chapter III showed that the habitat availability of large mammals, i.e., wild boar, moose, and wolf, increased in protected and unprotected habitats due to post-Soviet land-use change. In general, large mammals' habitat increased during the period 1987-2007, although differences emerged between the three protection zones of Oksky State Nature Reserve and its surroundings. The strictly protected core zone harbored the largest share of suitable habitat (at least 89% of the area), yet increase of that share was limited. The protection zones neighboring the core zone, i.e., the transition and buffer zone, yielded a lower share of large mammals' habitat compared to the core zone, but a larger increase over time (e.g., plus 26% for wolf). The surroundings of Oksky State Nature Reserve showed the largest increase in large mammals' habitat (e.g., plus 27% for moose), as post-Soviet land-use change, particularly farmland abandonment with subsequent natural succession, mainly occurred in unprotected areas.

In summary, protected areas in European Russia were effective in limiting forest logging before and after the breakdown of the Soviet Union. These findings are in line with similar, contemporaneous studies on strictly protected areas in other regions of European Russia (Wendland et al. 2015) and the Caucasus (Bragina et al. 2015b). Furthermore, the habitat availability of large mammals increased due to reduced land-use pressure and natural succession on abandoned farmland, and increased the share of suitable habitat in protected and unprotected areas.

Research question III: *How did the breakdown of the Soviet Union, and here in particular the interaction between land-use change and hunting, affect wildlife dynamics in European Russia?*

Chapter IV aimed at depicting the population dynamics and identifying the most determinant drivers of large mammals by using wild boar in Ryazan Oblast as an example for a large mammal species abundant in temperate European Russia. Particularly, the focus was on identifying the relative importance between different human drivers, i.e., land-use change and hunting, on wildlife dynamics in post-Soviet European Russia.

Chapter IV showed that wild boar abundance was changing in the period 1989-2010 in temperate European Russia, first, considerably declining until 1995 (-82%), and subsequently increasing until 2.5 times the population size of 1989 in 2010. Wolf population also substantially changed by first increasing to a maximum in 1999, and subsequently decreasing to a minimum in 2010 with only 0.3 times the population size of 1994. Regarding wild boar population dynamics, various factors related to hunting pressure, habitat and resource availability as well as natural mortality were consistently significant drivers of wild boar trends in both models, which covered the time periods 1989-2010 and 1999-2010, respectively.

Chapter IV also showed that official hunting did not limit increasing wild boar population dynamics after 1999, yet was rather positively related to population trends. Assuming that the effect of legal hunting on wild boar was similar in terms of not limiting population size during the 1990s, when wild boar abundance was considerably declining, provided evidence that illegal hunting must have strongly impacted wild boar populations during this time. Hunting-related factors were thus significant drivers of wild boar trends across both time periods after the breakdown of the Soviet Union until 2010. In contrast to that, farmland abandonment positively influenced wild boar trends only until 1998 and had no significant effect on population size after 1999. According to these results, hunting and poaching outweighed habitat-related factors in driving large mammal population dynamics in terms of significance across time.

In summary, the breakdown of the Soviet Union significantly affected wildlife dynamics in European Russia. First, a common set of essential factors describing human impact regarding hunting and land use, habitat and resources, and natural mortality significantly influenced large mammal abundance, which substantially changed over time. Second, hunting pressure, particularly due to illegal hunting, was of relatively higher importance for large mammals' trends than habitat-related factors.

2 Main conclusions

In the Anthropocene era with its ongoing biodiversity crisis, there is immense need for fostering nature conservation (Rands et al. 2010; Caro et al. 2012). The breakdown of the Soviet Union provided a large-scale quasi-natural experiment, which induced changes in the way how humans interact with their environment. Evaluating its effects on the interactions between land use, protected area effectiveness, and wildlife dynamics helps to reflect the impact humans have on biodiversity and nature conservation. This will support efforts to halt biodiversity loss and strengthen conservation initiatives. Based on the findings of the presented research four main conclusions can be drawn, which address the overall aim of this thesis:

1: The breakdown of the Soviet Union resulted in widespread land-use change that positively affected wildlife habitats and populations in European Russia. The aftermath of the breakdown of the Soviet Union triggered socio-economic and institutional changes, which affected land use and consequently wildlife habitats and populations in post-Soviet European Russia. The interaction of farmland abandonment, natural succession on abandoned land, and reduced forest logging resulted in time-lagged rewilding in the broader landscape of temperate European Russia. This post-Soviet rewilding positively affected both large mammals' habitat, which increased in post-Soviet times, and large mammals' population dynamics as a consequence of reduced human land-use pressure. The mutual assessment of changes affecting land-based systems such as agriculture and forestry thus revealed important information for nature conservation.

2: The breakdown of the Soviet Union resulted in changing hunting pressure, which was of higher relative importance for large mammals' population dynamics than habitat-related factors in post-Soviet times. Hunting pressure, a top-down driver directly affecting large mammals' population trends, was high yet changing over time in European Russia. First, likely due to the unknown, but widely assumed large share of illegal hunting. After the breakdown of the Soviet Union, illegal hunting was prospering due to severe socio-economic conditions of local people, restructuring of institutions responsible for game management and nature protection, and weak law enforcement. Second, due to the quota-based official hunting that is depending on the abundance of a particular game species and therewith susceptible to variation. Discriminating the effects of post-Soviet human impact on wildlife population dynamics revealed that hunting was of higher relative importance compared to the time-lagged effects of habitat change. This gained important information about the relation between top-down, i.e., hunting, and bottom-up, i.e., land-use change, factors influencing population dynamics, which are key drivers of global biodiversity loss.

3: Strictly protected areas in European Russia played an important role in halting threats to biodiversity in post-Soviet times despite institutional changes and widespread land-use change within their zone of interaction, yet accomplished to increase their effective area. In human-dominated areas, strictly protected areas often harbor remnants of natural areas, which serve as ecological baselines without any human impact. After the breakdown of the Soviet Union, strictly protected areas in temperate European Russia in most cases effectively prevented human-induced land-use change such as forest logging within their boundaries. They proved not being 'paper parks' in times of reduced funds for nature conservation and institutional restructuring, which is not given for all protected areas in post-Soviet European Russia (Wendland et al. 2015). Moreover, the strictly protected areas served as wildlife refuges in terms of hunting, which is usually prohibited within their areas. However, also effective protected areas rely on the surroundings in which they are embedded in, particularly in case of large mammals, which require a habitat size often exceeding that covered by the protected area. In post-Soviet times, human impact affected wildlife habitats and populations within and outside protected areas. Widespread land-use change with time-lagged rewilding happened within the protected areas' zone of interaction, especially within their surroundings, and resulted in an increased availability of large mammals' habitat in protected and unprotected areas over time. The breakdown of the Soviet Union hence resulted in the expansion of the protected areas' effective area for large mammals. This was accomplished by increasing habitat and the overall reduced land-use pressure in the zone of interaction, which aligned the protected areas themselves and their surroundings in this regard. This expansion of the effective area similarly benefitted biodiversity and wildlife species in protected and unprotected areas, especially large mammals.

4: Combining different data and interdisciplinary approaches revealed a reliable strategy to assess questions related to the human impact on biodiversity and highlighted the importance of long-term biodiversity data. This thesis used various spatial and non-spatial data covering geographical, ecological, and socio-economic aspects of the coupled human-environment system. These datasets were assessed by applying selected state-of-the-art tools from remote sensing, conservation biology and econometrics to assess the effects of the breakdown of the Soviet Union on the interaction of land-use change, protected area effectiveness, and wildlife dynamics. This thesis is one of the first studies comprehensively evaluating long-term Russian biodiversity data based on winter track counts, which were provided by strictly protected areas and hunting organizations in European Russia. These data are exceptional in terms of their large spatial and temporal coverage as well as their standardization. They offer an immense potential to unravel long-term trends in ecosystems and wildlife abundance in coupled human-environment systems as short-term trends co-occur, especially when combined with other data. Additional information provided, for example, by time series of satellite images, climate data, and socio-economic statistics, can help to identify the effects of socio-economic and institutional shocks. This has the potential to support biodiversity monitoring and overcome knowledge gaps on biodiversity conservation.

3 Implications

The findings of this thesis have the potential to enhance the scientific expertise related to questions and challenges in biodiversity conservation and provide information to decision-makers in guiding conservation actions and sustainable land-use strategies. They contribute to a better understanding of how socio-economic and institutional shocks in coupled human-environment systems affect biodiversity and nature conservation. This thesis thus gained new insights along the goals of the Convention on Biological Diversity (CBD) to conserve biodiversity and sustainably use its components (UN 1992, Article 6) and can be linked to the Aichi Biodiversity Targets (ABT) aiming to reduce future biodiversity loss and to improve biodiversity monitoring.

First, this thesis contributed to research addressing the underlying causes of biodiversity loss by evaluating the impacts of a rapid shock in socio-economic and institutional conditions on land use, protected area effectiveness, and wildlife dynamics (ABT, Strategic Goal A). As rapid shocks are hard to predict, the findings of this thesis can be used to learn about challenges and opportunities for biodiversity in times of unexpected incidents in socio-economic and institutional conditions. The findings can furthermore be used as input for future-scenario models of biodiversity to limit uncertainty due to shocks in coupled human-environment systems.

Second, this thesis provided information on changes in wildlife habitat and population dynamics due to human impact, particularly land-use change and hunting, and their relative effects on wildlife dynamics. It thus essentially contributed to inform about key drivers of biodiversity loss. Such information is often lacking at relevant scales (EEA 2015), yet strongly required to reduce direct pressures on natural habitats (ABT, Strategic Goal B, Target 5).

Third, this thesis has the potential to inform decision-makers on sustainable land management to ensure biodiversity conservation (ABT, Strategic Goal B, Target 7). The findings of this thesis revealed that reduced human impact benefitted wildlife, particularly in terms of large mammals' habitat due to post-Soviet farmland abandonment. Recently, areas of abandoned farmland have gained importance in terms of recultivation as several studies are highlighting for Eastern Europe and Kazakhstan (Estel et al. 2015; Kraemer et al. 2015; Meyfroidt et al. 2016). Potential underlying drivers of recultivation are first, increasing global demands on products from land-based systems such as agriculture and forestry, and second, multifaceted international political and economic relations, which can result in sudden changes of trade relations, for example, the Russian import ban on agricultural products from certain western countries in 2014. In this regard, this thesis contributed information on the high value of abandoned and rewilded areas for wildlife and may help decision-makers to decide on a sustainable balance between productive and protected land areas to support sustainable land management and safeguard biodiversity.

Fourth, this thesis provided information that help to identify areas suitable for expanding the network of protected areas in order to improve the status of biodiversity (ATB, Strategic Goal C, Target 11). The findings of this thesis showed that the effective area of strictly protected areas increased within their zone of interaction due to widespread reduced land-use pressure and rewilding in European Russia. Transferring these areas to the legal management of protected areas provides one opportunity to fulfill the targeted share of 17% protected terrestrial and inland water in Russia until 2020. Increasing the protected area in Russia, however, will contribute to, not solve the global problem of biodiversity loss, especially regarding projected future land use and derived conservation priorities (Pouzols et al. 2014).

Finally, this thesis has the potential to contribute to capacity building in biodiversity monitoring (ATB, Strategic Goal E, Target 19). The findings of this thesis were based on a broad range of data and interdisciplinary approaches to monitor and evaluate changes in land use and hunting pressure, protected areas, wildlife habitats, and species population dynamics. In terms of data, this thesis has the potential to support global efforts to assemble a global and standardized monitoring system using 'Essential Biodiversity Variables' (EBVs) to timely inform about biodiversity change as it assessed long-term data sets informing about ecosystems and species populations (Butchart et al. 2010; Pereira et al. 2013). The findings of this thesis especially highlighted the exceptional value of Russian biodiversity data in evaluating long-term biodiversity changes. However, the current state and future of the Russian data archive is largely unknown and enormous efforts in financial and human resources are necessary to maintain the archive for future generations. In terms of approaches, this thesis presented interdisciplinary research that is repeatable for other regions and species as it was including freely available remote sensing data and state-of-the-art tools in remote sensing, effectiveness analysis, and modelling of species habitats and population dynamics. Especially remote sensing data and tools show increasing capabilities to monitor the implementation progress of the Aichi Biodiversity Targets as new opportunities of satellite sensors for species conservation emerge (He et al. 2015; O'Connor et al. 2015).

4 Outlook

The findings of this thesis can be used to support biodiversity monitoring and to overcome knowledge gaps on biodiversity conservation. This work provided a considerable contribution in better understanding the effects of the socio-economic and institutional shock following the breakdown of the Soviet Union in 1991 on land use, protected area effectiveness, and wildlife dynamics in European Russia. During the course of this thesis, however, some relevant subjects for follow-up research emerged that were beyond the scope of this work.

With regard to the assessment of land-use change, the study could benefit from extending the spatial and temporal scales of this thesis. First, several studies emerged during the course of this thesis, which evaluated changes in land use by covering a study area exceeding the temperate region of European Russia, for example, regarding farmland abandonment (Prishchepov et al. 2012a; Estel et al. 2015) or changes in forest cover (Baumann et al. 2012). The study by Potapov et al. (2015) provided a mutual assessment of both aspects of land-use change, and related results could be used to assess large-scale landscape fragmentation to better inform about landscape and habitat connectivity, which are especially important for large mammals. Second, extending the study period would help to assess impacts on biodiversity beyond the aftermath of the breakdown of the Soviet Union. One such example is the severe drought in European Russia in 2010, which resulted in widespread wildfires affecting large regions and wildlife habitats. Furthermore, an extended study period would allow making full use of the long-term Russian biodiversity data, which happen to date back until the 1960s. Third, this study did not include future scenarios on land use, which is of high interest in times of globally growing demands of agricultural outputs. Recent studies evaluated the potential of recultivating abandoned farmland in countries of the former Soviet Union (Kraemer et al. 2015; Meyfroidt et al. 2016). These studies can provide a baseline to evaluate impacts of future land-use change on new wildlife habitats, which were gained in post-Soviet times and positively influenced large mammals' population dynamics in European Russia.

Follow-up applications regarding protected area effectiveness may focus on a broader set of threats affecting protected areas and assess the quality of the Russian network of protected areas. First, there are other threats besides forest logging that impact the effectiveness of protected areas in reducing threats to the protected ecosystems and wildlife. In case of Oksky State Nature Reserve, second house building, which occurs within and outside the protected area increases human impact on natural areas and may affect wildlife habitats and result in increased isolation (Radeloff et al. 2010). Furthermore, climate change can shift species distributions beyond protected areas (Hannah et al. 2007). Long-term trends of weather data depicted changing climate in temperate European Russia (Onufrenya 2003), what is particularly important for Oksky and Mordovsky State Nature Reserves as they are located at the junction of two ecoregions. Second, conservation of wildlife and large mammals in particular, requires well-connected protected areas, especially in human-dominated areas (Ripple et al. 2014). Assessing the connectivity of the Russian network of protected areas in terms of habitat could contribute essential information on the status of large mammals' conservation in the largest country of the world, similarly to other large-scale approaches (Wegmann et al. 2014). Including different types of protected areas managed at the federal, regional and local level into such an analysis would add further knowledge on how effective the Russian network of protected areas is regarding the connectivity of protected and unprotected natural habitats.

Future research in terms of wildlife dynamics could cover further species of interest and include additional factors likely to change population trends. First, further species could be included into the analyses, particularly game species or large mammals of conservation concern, e.g., brown bear, to learn from more examples about the interrelated effects of post-Soviet land-use change and hunting pressure on species' population dynamics. Second, not all factors influencing wildlife dynamics were covered in this thesis. Especially future scenarios would be helpful to further elaborate the effects of human impact on wildlife. This could be done via including projected socio-economic conditions or future land-use change and changing climate, which is particularly affecting large mammals (Craine et al. 2015), and would help to advance our knowledge on the coupled human-environment system and on future threats to biodiversity.

In summary, this thesis revealed knowledge at the connection of multiple research disciplines, which are all contributing to learn about key drivers of biodiversity loss. This work demonstrated the value of interdisciplinary research and provided links for future research aiming to further support biodiversity conservation.

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PEER-REVIEWED JOURNAL ARTICLES

In review

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Bragina, E., Shchur, A., Pidgeon, A., Radeloff, V.C., **Sieber, A.** (2016): Mapping Selective Logging And Clearcuts In Protected Forests Of Western Siberia, Using Landsat Summer And Winter Imagery. Society for Conservation Biology (SCB) 3rd North American

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Sieber, A., Kuemmerle, T., Baskin, L.M., Uvarov, N.V., Prishchepov, A.V., Radeloff, V.C., Jones, K.W., Hostert, P. (2016): Land-use change, protected area effectiveness, and wildlife dynamics in post-Soviet European Russia. European Space Agency (ESA) Living Planet Symposium 2016. Prague, Czech Republic, May 09-13. *Poster presentation.*

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Eidesstattliche Erklärung

Hiermit erkläre ich, die vorliegende Dissertation selbstständig und ohne Verwendung unerlaubter Hilfe angefertigt zu haben. Die aus fremden Quellen direkt oder indirekt übernommenen Inhalte sind als solche kenntlich gemacht. Die Dissertation wird erstmalig und nur an der Humboldt-Universität zu Berlin eingereicht. Weiterhin erkläre ich, nicht bereits einen Doktortitel im Fach Geographie zu besitzen. Die dem Verfahren zu Grunde liegende Promotionsordnung ist mir bekannt.

Anika Sieber

Berlin, den 29. Juli 2016